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Sound Production in Longear Sunfish (*Lepomis megalotis*):

Acoustic Behavior and Geographic Variation

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Sound Production in Longear Sunfish (*Lepomis megalotis*): Acoustic Behavior and Geographic Variation

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Sound Production in Longear Sunfish (*Lepomis megalotis*): Acoustic Behavior and Geographic Variation

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Acoustic communication during reproductive behavior of longear sunfish (*Lepomis megalotis aquilensis*, Centrarchidae) was studied in streams in central Texas. Longear sunfish, with documented ecology and behavior, are an ideal model system to study geographic divergence and the forces driving it. Calls collected from five streams around Austin, TX (*L. m. aquilensis*) and from Brier Creek, OK (*L. m. breviceps*) were used to examine variation within individuals, among individuals from the same population, among populations of the same subspecies and between subspecies. Analysis of animal calls that are low frequency and short duration can be imprecise using traditional Fourier-based techniques. The results

from wavelet and Fourier transforms were compared using a variety of animal calls and synthetic signals in order to assess accuracy and precision. Longear sunfish parental males produce both courtship and pursuit calls while nesting. Courtship calls are directed toward females and are given in conjunction with a distinctive visual courtship display. Pursuit calls are typically directed toward 'raiders' and are given during pursuits. The amount of variation in pulse rate and frequency differs between contexts, with pursuit calls exhibiting more variation. Ambient noise and acoustic signal propagation were measured at each of the study sites, with urban sites having higher ambient noise than sites in nature preserves. A series of pure tones and longear sunfish call exemplars were played at each site to assess signal propagation. In general, 75 - 200 Hz attenuated least in all these shallow streams indicating a 'window' for signal propagation. Fish appear to take advantage of signal propagation windows generated by near field effects for acoustic communication. Nested MANOVAs reveal significant differences among males within a population and among populations for both pursuit and courtship calls. Pursuit calls from males appear to be less different than courtship calls among sites. Microgeographic variation in acoustic signals has not been documented in fish before.

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Chapter 1

Introduction

Communication systems provide good models for studying evolution because the integrative nature requires an understanding of physiology, morphology, behavior and genetics, and because they are fundamentally a problem in coevolution between sender and receiver (Ryan 1988). Communication occurs when a sender conveys information to a receiver. There have been various discussions as to the specifics of the information, the intentions, the receiver, and the conditions involved in communication (Hauser 1996; Vehrencamp & Bradbury 1998). Almost all definitions have in common a sender producing a signal, typically specialized, that provides information to a receiver (or receivers) for the purposes of affecting the receiver's behavior in a specific behavioral context (Hauser 1996; Wilczynski & Ryan 1999). Communication is used in many different behavioral contexts, but it is especially important during reproduction in many species. Especially in species with parental care, where mistakes are costly, all forms (visual, acoustic, olfactory, tactile) of communication are often used during mate choice (Hauser 1996; Vehrencamp & Bradbury 1998).

Acoustic communication in fishes has rarely been examined beyond basic descriptions and few field studies have been conducted. However, it is clear from

the basic descriptions that the use of acoustic communication is widespread among fishes (Bass et al. 1997; Bright 1972; Fish & Mowbray 1970; Johnson 2000; Ladich 1997a; Lugli et al. 1997). Almost all fish calls, with a few estuarine exceptions, are pulsatile, low frequency, and broad band in acoustic structure. They are typically used during courtship or territory defense by territorial, reproductively mature males. The extensive geographic variation typical of freshwater fishes in morphology, color and behavior provides an opportunity to study signal function and evolution within a species or genus. A thorough understanding of acoustic communication in at least a few species would provide useful comparisons to terrestrial systems in frogs and insects and help develop broader principles of signal design and evolution that are not habitat or taxon specific.

Given the diversity of mechanisms present in fishes, ranging from gasbladder muscles, fin ray and spine modifications, and pharyngeal teeth in fishes (Bass et al. 1994; Fine et al. 1996; Fish & Mowbray 1970; Ladich & Fine 1992; Lanzing 1974; Moyle & Cech 1999), compared to frogs, birds and mammals which produce sound using either a larynx or syrinx, and the different environment, comparisons between communication systems in aquatic and terrestrial systems might yield some new insights. The diversity of mechanisms in fishes and invertebrates allows for more independent contrasts to study the evolution of sound production and acoustic communication. Then, the evolutionary patterns that

emerge can be compared to evolutionary patterns in terrestrial organisms to reveal broad patterns in signal evolution and behavioral evolution.

The state of the field and patterns of acoustic communication in fishes will be discussed. The basic biology of sunfish will be summarized, focusing on behavior, ecology and evolution. A brief summary of each chapter follows and, finally, a discussion of questions raised by this research and potential future research projects is undertaken. This introductory chapter is meant to provide a framework for the following chapters. Each chapter also has an introductory section with relevant background information.

ACOUSTIC COMMUNICATION IN FISHES

Almost all research on acoustic communication in freshwater fishes focused on captive, laboratory specimens and/or the neurobiology of sound production and reception. Approximately every five years, sound production is reported in a 'new' family or genus (e.g. Colson et al. 1998; Johnson 2000; Ladich & Tadler 1988; Mann et al. 1997). Given the lack of basic surveys for and descriptions of sound production, there are few studies that go into more depth. Notable exceptions include the detailed neuroethological research on midshipman, *Porichthys notatus*, (Bass 1992; Bass et al. 1996, 1997; Brantley & Bass 1994), the extensive behavioral research on Italian freshwater gobies (Lindström & Lugli 2000; Lugli et al. 1996;

Torricelli et al. 1986, 1990) and on weakly electric fish, *Pollimyrus* species (Crawford et al. 1997; Crawford & Xiaofeng 1999). There are now enough descriptive reports, however, that some general patterns are emerging.

The following discussion will focus primarily on freshwater and coral reef fishes, as open water marine and estuarine fishes experience different environmental acoustics and appear to use acoustic signals for different purposes. Open water marine fishes seem to use acoustic signals in social behaviors, such as schooling, as well as for distress and reproduction (Fish & Mowbray 1970). Estuarine fishes seem to use acoustic signals for both long and short distance communication, primarily during the breeding season (Brantley & Bass 1994; Fine 1978; Fish & Mowbray 1970). The majority of, if not all, freshwater fishes and most coral reef fishes appear to use acoustic signals for only short distance communication (Johnson 2000; Ladich 1997a; Myrberg 1997a).

Coral reef and freshwater fish calls tend to be pulsed, broad band, low frequency signals used by territorial males during courtship and agonistic behavior (Ladich 1997a; Myrberg 1981; 1997b; Schwarz 1985). Fishes living in both clear and murky water, shallow and deep water, open and vegetated water, use acoustic signals to communicate. Not only does acoustic communication occur across in a wide variety of habitats and taxa, but the mechanisms used for sound production vary among clades (Alexander 1966; Ladich 1997a, b). A substantial portion use a

gasbladder-based mechanism, but with a wide diversity in the physiology (Fish & Mowbray 1970; Helfman et al. 1997; Moyle & Cech 1999). Some taxa use muscles directly attached to the gasbladder, others use bones or tendons to snap against the gasbladder. Other taxa use diverse stridulatory mechanisms ranging from fin spines to tendons connected to fins to pharyngeal teeth (Fine et al. 1996; Fish & Mowbray 1970; Kaatz & Stewart 1996; Ladich & Fine 1992). For many freshwater species the production mechanism is unknown; in other words, it is not the gasbladder or fin spine mechanism as these are easy to identify, and the actual mechanism has not been determined.

Family	Context	Type of Call
Callichthyidae	Courtship, Agonistic	rasps and knocks
Cyprinidae	Courtship, Agonistic	knocks
Fundulidae	Courtship	drums and knocks
Cyprinodontidae	Courtship, Agonistic	drums and knocks
Mormyridae	Courtship, Agonistic	grunts, moans, hoots
Gobiidae	Courtship, Spawning	drumming
Cichlidae	Courtship, Agonistic	growls
Centrarchidae	Courtship, Agonistic	grunts and knocks
Belontiidae	Courtship, Agonistic	croaks
Percidae	Courtship, Agonistic	moans and knocks

Table 1. Representative freshwater fish families in which sound production has been documented. Based on (Crawford et al. 1997; Drewry 1962; Gerald 1971; Johnson 2000; Johnston & Johnson 2000; Kaatz & Stewart 1996; Ladich 1997a; Lugli et al. 1997; Schwarz 1980)

BASIC BEHAVIOR, ECOLOGY AND EVOLUTION OF SUNFISH

Basic reproductive behavior, habitat use and typical diet, as well as the evolutionary relationships of *Lepomis* sunfish, are summarized to provide background for the following chapters. Longear sunfish (*Lepomis megalotis*, Centrarchidae, Perciformes, Teleostei) are a good model system because they are abundant, easy to identify, easy to observe, and relatively easy to catch. Parental male longear sunfish remain highly localized once mature and may nest at the same location each year (Gunning & Shoop 1963; Ross & Baker 1983). There is a large body of research on sunfish systematics, behavior, ecology and physiology although little is known about their acoustic communication, except that they use acoustic signals in courtship encounters during the reproductive season (e.g. Drake et al. 1997; Ehlinger et al. 1997; Etnier 1971; Gerald 1971; Mabee 1995; Miller 1963; Rabeni 1990; Sadzikowski & Wallace 1976). There are two studies of acoustic communication in Centrarchid fishes. Gerald (1971) first described sounds in *Lepomis* and focused on differences in courtship calls among several species in central Texas. Ballantyne & Colgan (1978a, b, c) examined hybrids and assessed the use of, and response to, acoustic signals in two species, *L. gibbosus* and *L. macrochirus,* and their hybrids (see Chapter 3 for a detailed summary). Neither study addressed the structure, function and diversity of the acoustic signals.

The basics of reproductive behavior in longear sunfish are similar to other *Lepomis* species (e.g. Breder Jr. 1936; Gross 1982; Witt Jr. & Marzolf 1954), beginning when daylight and water temperature increase in the spring. Males establish territories, either colonially or solitarily, build and guard nests in shallow, clear, flowing water (Dupuis & Keenleyside 1988; Jennings & Philipp 1992). Females approach nests during the day and eventually mate with one or more males. Upon sighting a female, a male will approach and try to lead her to the nest. In addition to nesting territorial males, small non-territorial sneaker males try to steal fertilizations by sneaking up to a spawning pair. On occasion (rare in Texas), a sneaker male or young parental male will attempt to 'mimic' a female and infiltrate a spawning event (Gross 1982). Neighboring males also attempt to steal fertilizations on occasion (Keenleyside 1972). Sneaker males, reproductive females and non-reproductive individuals are found around colonies as 'raiders' that attempt to eat eggs and larvae from nests. Following spawning, the female leaves the nest area and the male cares for the eggs and larvae by fanning, removing fungus and invertebrates, and chasing off intruders.

CHAPTER SUMMARIES

Chapter 2 describes the methods used to analyze the low frequency, short duration, broad band calls produced by longear sunfish and other fishes. The

damped sinusoid wavelet used throughout this dissertation is compared to the traditional Fourier transform using both synthetic signals and real calls from fishes, frogs and a cricket. While wavelets are useful in a wide variety of circumstances, I believe they are most useful with fish because most fish calls are low frequency, short duration calls. I propose some guidelines for determining whether wavelets are appropriate and/or necessary to analyze a given signal.

Chapter 3 describes the behavior associated with sound production in longear sunfish. Descriptions of sender and receiver behavior during both courtship and pursuit calls are provided. A comparison of calls between contexts and correlations among call parameters are provided. Functions of the calls are postulated and similarity of sound production in longear sunfish and other fishes is discussed. Courtship calls seem to be similar to advertisement calls in frogs, while pursuit calls seem to be similar to release calls in frogs.

Chapter 4 summarizes data on habitat acoustics from six study sites in central Texas. Ambient noise and signal propagation are compared across frequencies from different sites. Interestingly, the majority of ambient noise is below 100 Hz while the window of best signal propagation is between 75 - 200 Hz. With the majority of energy in longear sunfish calls between 75 - 300 Hz, the sunfish seem to be avoiding the highest ambient noise and using a window available for short range communication in streams.

Chapter 5 summarizes variation in calls within individuals, among individuals within a site, and variation among sites. Various explanations for this geographic variation are explored, such as shared acoustic space, habitat differences, and gene flow. Variation is lowest for temporal parameters which might indicate that timing is constrained by the production mechanism compared to dominant frequency, in contrast to research in frogs.

FUTURE RESEARCH/QUESTIONS RAISED

Other than in guppies, (Endler 1995; Houde & Endler 1990), sticklebacks (Rundle & Schluter 1998; Schluter 1993; Schluter & McPhail 1992) and swordtails (Ryan 1992; Ryan et al. 1992), there are few field studies that attempt to understand what causes geographic behavioral variation in freshwater fishes. Given the not infrequent cases of sympatric divergence and speciation that appear in freshwater fishes (Skulason & Smith 1995; Thompson et al. 1997; Wood & Foote 1996), an understanding of what drives variation in behavior across watersheds could not only help explain allopatric divergence but might lend insights into forces at work in sympatric divergence as well. My research focused on *L. m. aquilensis* with a few individuals from *L. m. breviceps*. Longear sunfish, however, occur from Ontario to Mexico with substantial color, morphological and genetic variation across the range, and similar variation in acoustic signals would not be surprising. A

comparative study across the seven subspecies of longear sunfish would help elucidate the evolution of acoustic communication within a species.

Gerald (1970, 1971) found that all other *Lepomis* species in Texas use acoustic signals, except the redbreast sunfish. The redbreast sunfish does as well, but only pursuit calls (pers. obs.). With the extensive description furnished here, a comparative study examining signals and behavior in other *Lepomis* species will yield a solid framework for understanding evolution of acoustic communication in an aquatic group. Gerald's (1971) work indicates divergence in pulse rate and pulse duration in courtship calls among species. One would predict that pursuit calls are similar across all taxa since sunfish often form multi-species colonies and raiders are individuals from all the *Lepomis* species. However, the courtship calls should show varying degrees of divergence depending on how likely species are to nest near each other and possibly how closely the species are related. Combining the inter-species and intra-species comparative studies would yield a robust and informative data set.

The discrepancies between the damped sinusoid wavelet results and the Fourier results raises questions regarding the accuracy of previous data on low frequency, pulsed fish calls. Fourier transforms of these calls do not provide the resolution needed to accurately depict the signal. Results to date indicate that frequency is not as important a cue in aquatic systems as temporal patterning

(Myrberg et al. 1978; Schwarz 1985). The lack of reliance on frequency may be due to the technical difficulty of accurately quantifying frequency, especially as most fish calls are broad band or maybe fish cue on a different aspect of frequency than terrestrial organisms. There may be a constraint on the sensory or production systems that limits the ability to generate reliable frequency information. A constraint on production seems unlikely as there is an astounding diversity of independently derived mechanisms across a broad array of taxa (e.g. Bass 1989; Ladich 1997b; Ladich & Fine 1992). Or it could simply be that frequency information is unreliable in underwater signals, while temporal information has higher fidelity, so therefore there has not been selection to produce reliable frequency information.

The comparison of signal propagation across five sites in this study is an important step toward understanding signal propagation in extremely shallow water. To date, there has been little focus from the theoretical standpoint on how sound travels through shallow water. The fact that the same signal propagation properties are seen across these five sites with varying substrates and stream depths and widths generates some intriguing questions. Do sunfish locate their colonies in parts of the stream where their signals propagate best? Extensive mapping within one stream would be necessary to answer this question. If there really is little variation in signal propagation, why? Theory indicates there should be substantial variation due

to variation in substrate, temperature and stream width across sites (Richardson et al. 1995; Urick 1983). If this window of 75 - 200 Hz is present across a wide variety of streams, it could certainly explain why so many freshwater fish calls have similar design with dominant frequencies below 400 Hz and broad band, pulsed signals.

Finally and most intriguingly, does noise pollution interfere with communication or affect evolution of signals? It is certainly present in some of these streams, especially Waller Creek, and many species still reproduce successfully with large populations. A recent study documented reduced hearing ability after exposure to noise in fathead minnows (*Pimephales promelas*) (Scholik & Yan 2001). Are urban stream fishes slightly deaf compared to other populations? How are urban stream fishes adjusting to this extreme environment? What are the implications in terms of evolution of these populations?

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Chapter 2
Signal Analysis of Animal Calls: Comparison of Fourier and Wavelet Transforms

Analysis of low frequency and short duration animal calls using traditional Fourier-based techniques can be imprecise, especially for low frequency, short duration signals. Wavelet transforms provide an alternative means of analysis with higher precision and greater flexibility. Synthetic calls and calls from fishes, frogs and a cricket were used to compare the results of these two techniques. Each synthetic signal had five programmed frequencies, but only the two with the most energy (55 and 507 Hz) were never missed by any technique. As a general rule, analysis of calls with broad band structure and a duration less than 50 times the period will benefit the most from wavelet analysis as these are the type of signals with poorest resolution in Fourier analysis. The increase in resolution from wavelet analysis is particularly useful for studies investigating the mechanism of sound production.

INTRODUCTION

The structure of low frequency, short duration calls is difficult to elucidate using standard bioacoustics techniques based on Fourier transforms, since they do not provide precise results for transient, broad band, low frequency signals (Bruce

et al. 1996; Graps 1995; Mallat 1999; Perrier et al. 1995; Rioul & Vetterli 1991). I compared a damped sinusoid wavelet transform with the traditional Fourier transform for analyses of animal communication signals (Figure 1). The damped sinusoid wavelet is relatively similar to the standard sine wave used in Fourier analysis and it is representative of many sounds produced by animals, especially those using vibrating membranes or masses (Burrus et al. 1998; Cohen & Kovacevic 1996; Graps 1995; Mallat 1999; Priebe 1995).

Fourier transforms, the traditional spectral analysis tool in bioacoustics, extract frequency information by comparing the signal of interest with infinite sine and cosine waves. A critical assumption of Fourier analysis is that the signal of interest is a periodic, stationary signal with a waveform similar to a sine wave (Bruce et al. 1996; Graps 1995; Mallat 1999; Perrier et al. 1995). This assumption is violated if the duration of the signal is short, especially if it is only slightly longer than the period. This can be partially compensated for by using an appropriate window length with overlap. However, the same window length is used for all frequencies, which leads to a Fourier 'uncertainty principle' - there can either be good frequency resolution or good time resolution but not both (Bruce et al. 1996; Graps 1995; Mallat 1999; Perrier et al. 1995). Most fish calls and many other animal calls violate the assumptions of Fourier analysis because they are transient, non-stationary, non-periodic, broad band signals with a short duration. As a result,

while Fourier analysis may provide a reasonable estimate of dominant frequency in some cases, it provides little or no information about acoustic structure when the spectral characteristics change rapidly with time.

Wavelets were developed simultaneously in the 1980's by engineers, geologists and mathematicians to deal with exactly these problems (Bruce et al. 1996; Daubechies 1996; Graps 1995; Mallat 1999; Sweldens 1996). Since about 1991, wavelets have been used in an increasingly diverse array of fields including fingerprint compression, de-noising, signal reconstruction, and sound analysis (Bailey et al. 1998; Graps 1995; Hess-Nielsen & Wickerhauser 1996; Priebe 1995). Wavelet transforms are widely used in medicine for analysis of heartbeats and various other signals (e.g. Akay 1997; Lotric et al. 2000; Mallat 1996; Senhadji et al. 1995; Unser & Aldroubi 1996; Williams 1998). However, wavelet transforms are still not used widely in the study of animal communication.

Wavelet transforms and Fourier transforms are used in a similar manner: an analyzing signal is compared to a signal of interest to extract spectral information. Indeed, the sine wave used in Fourier transforms is simply one type of wavelet. Wavelet transforms provide many advantages for signal analysis. First, one is not restricted to infinite, or even windowed, sine waves. The wavelet can be any waveform, but for optimal resolution it should match the waveform of the signal of interest. An important and timesaving outcome is that the analysis basically ignores

any signal that does not match the wavelet, so filtering is not required before extracting spectral information. Second, the window length used to analyze the signal varies based on frequency, so it is possible to obtain more accurate frequency and time information (Figure 1).

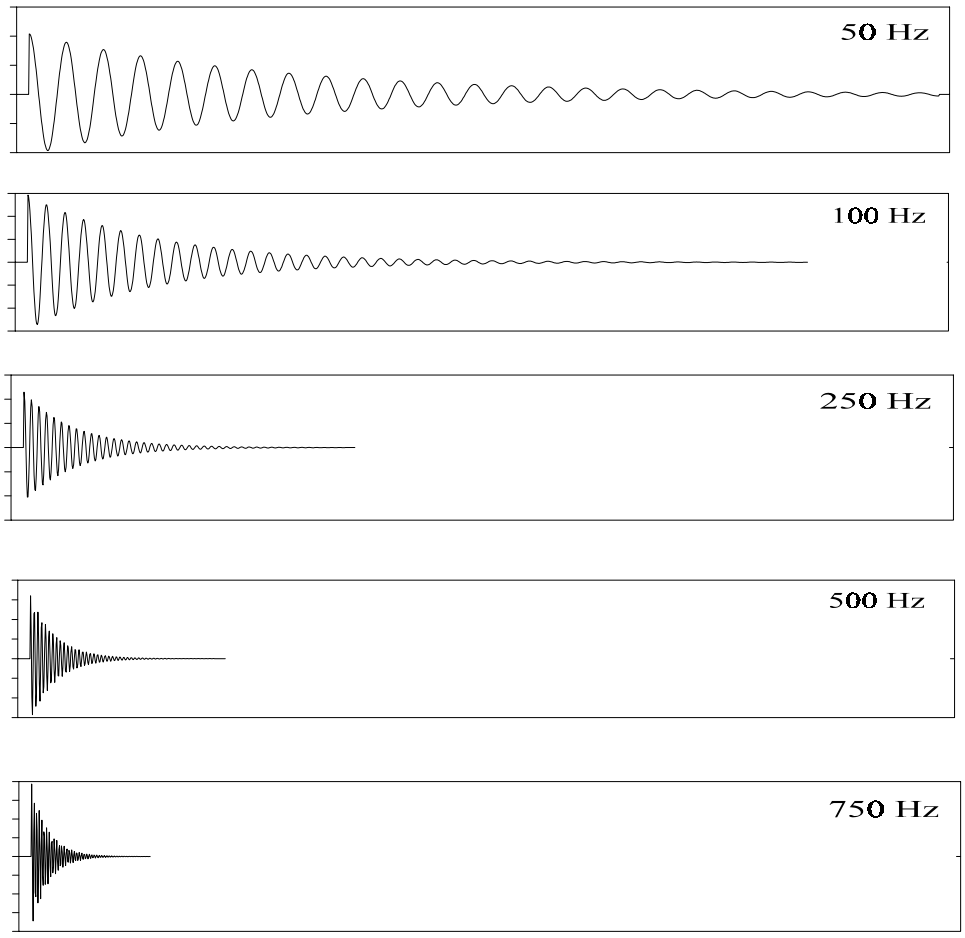

Figure 1. Partial series of damped sinusoid wavelets (damping rate -0.40) used in this analysis. The frequency indicated is the frequency for which this wavelet is used in the analysis.

In other words, instead of using the same duration sine wave for every frequency from 10 to 10,000 Hz, a longer wavelet of the same shape is used at 10 Hz relative to a shorter wavelet at 10,000 Hz. There is still some imprecision with lower frequencies having greater frequency resolution and higher frequencies having greater time resolution, however this imprecision is substantially less than traditional Fourier methods, and can be partially corrected by using even more complicated wavelet methods (Bruce et al. 1996; Graps 1995; Mallat 1999; Perrier et al. 1995; Rioul & Vetterli 1991). The difference in resolution between wavelet and Fourier transforms is particularly noticeable in short duration, low frequency signals (Akay 1997; Graps 1995; Mallat 1999). Wavelet transforms are more computationally intensive than Fourier transforms, but recent advances in computer technology have reduced the computational time difference from 30 minutes to 3 minutes for 3 second signal (pers. obs.). Many publications provide detailed explanations of the mathematical basis and advantages of wavelet transforms (e.g. Blinowska & Durka 1997; Burrus et al. 1998; Cohen & Kovacevic 1996; Graps 1995; Hess-Nielsen & Wickerhauser 1996; Mallat 1999; Priestley 1996; Rioul & Vetterli 1991; Starck et al. 1997).

The goal of this paper is to compare the results of Fourier transforms and damped sinusoid wavelet transforms on a variety of signals, both synthetic and real

animal calls. Guidelines for the use of wavelets are provided based on signal structure and analysis goals.

MATERIALS AND METHODS

Synthetic signals generated in MATLAB (Version 5.3 Release 11, The Mathworks Inc., 1999) consisted of one series of sine pulses and one series of gaussian pulses, each with components at 5 frequencies (55, 123, 202, 507 and 1110 Hz). The relative amplitude of each frequency and the duration of the pulse varied with 55 Hz as dominant frequency (F1) in half the series and 507 Hz as F1 in the other half (for examples see Figures 2 - 3).

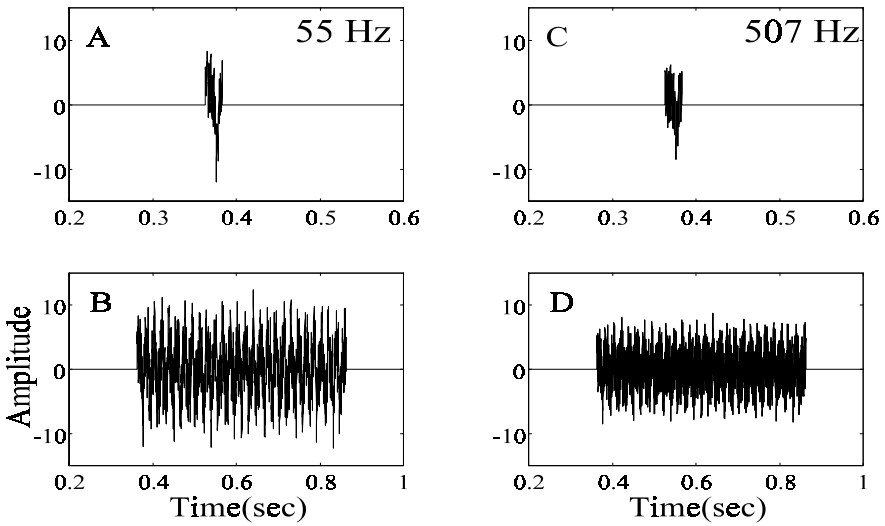

Figure 2. Examples of synthetic sine waves. On left (A, B) are signals with 55 Hz dominant frequency. On right (C, D) are signals with 507 Hz dominant frequency. The top panels (A, C) are 20 msec duration, bottom panels (B, D) are 500 msec duration .

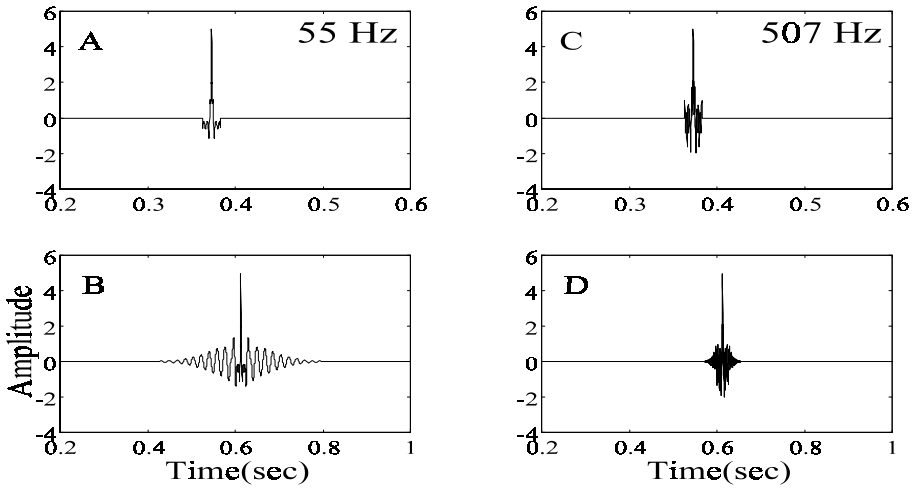

Figure 3. Examples of the synthetic gaussian pulses. On the left (A, B) are signals with 55 Hz as dominant frequency. On the right (C, D) are signals with 507 Hz as dominant frequency. The top panels (A, C) are 0.01 sec in duration, while the bottom panels (B, D) are 0.25 sec in duration.

Fish calls were recorded from longear sunfish (*Lepomis megalotis*) (D. Johnson, unpub. data), twoline pupfish (*Cyprinodon bifasciatus*) (Johnson 2000), bluntnose minnow (*Pimephales notatus*) (Johnston & Johnson 2000b), fringed and blackfin darters (*Etheostoma crossoptera, E. nigripinne*) (Johnston & Johnson 2000a), and spot-tail shiners (*Cyprinella venusta*) (D. Johnson, unpub. data). Calls from Hylid frogs (cricket frog, *Acris crepitans*, and green tree frog, *Hyla cinerea*) and a Leptodactylid frog (*Odontophrynus americanus*) were obtained from Marcos Papp (University of Texas at Austin, unpub. data). Cricket calls (*Gryllus integer*) were obtained from Laura Higgins (University of Florida at Gainesville, unpub. data). All calls were digitized at 44,100 samples/sec, filtered and re-sampled to

lower sampling rates (see Table 2 for processing parameters). Window lengths for Fourier analysis and upper thresholds for wavelet analysis depended on sampling rate and signal (see Table 2 for analysis parameters). The filtering and re-sampling removed most, if not all, harmonics in these calls. There are no harmonics in the fish calls.

Signal	High-Pass Filter (Hz)	Re-Sampling Rate (samples/sec)	Fourier Window	Wavelet Threshold (Hz)	Wavelet Damping Rate
Synthetic		5512.5	512	1,500	-0.15
Fish	1,500	2756.25	256	1,000	-0.15 & -0.40
Frogs & Cricket	10,000	22050	1024	10,000	-0.15, -0.40 & -0.05

Table 2. Summary of parameters for signal analysis in comparisons. Filter is lower threshold for high-pass filtering before re-sampling. Fourier window is the window length used in Fourier analyses. Wavelet threshold is the upper bound used in wavelet analyses. All calls were analyzed using 200 frequency bins for wavelet analyses.

All signal processing and analysis was performed in MATLAB and statistical analysis was performed in Systat (Version 10.0, SPSS Inc, 2000). A damped sinusoid wavelet (Figure 1) was used to analyze the sunfish calls with original code developed by Dr. Russell Priebe (Priebe 1995) that was adapted for fish call analysis. A damped sinusoid wavelet (Figure 1) is similar to the sine wave used in Fourier analysis, except that it is not infinite. A damped sinusoid wavelet is a

simple wavelet and is generally applicable to the majority of animal calls. This is true because the vibrating membranes used by many organisms to produce sound generate a damped sinusoid signal. It may not be the optimal wavelet for every signal in this analysis, but it is easily compared to the Fourier transform and, by adjusting the damping rate, provides a good example of the improved resolution offered by wavelet transforms. There are a variety of sources and software programs that help select the optimal wavelet (e.g. Senhadji et al. 1995).

Output from Fourier analysis was a power spectrum using the window length indicated in Table 2. Frequency peaks were then measured from the power spectrum (Figure 4). Output from wavelet analysis was multi-phased. The first step resulted in a three-dimensional spectrogram (Figure 5). Each frequency bin was summed across time to generate the power spectrum and frequency peaks were extracted (Figure 4). The last phase resulted in a set of modes for each call (Figure 6 and Table 3). Modes, which are localized energy peaks, were extracted based on the wavelet transform and frequency, peak time, duration, decay rate, and relative energy were determined for each mode. Relative energy was calculated by normalizing every mode by the mode with the most energy.

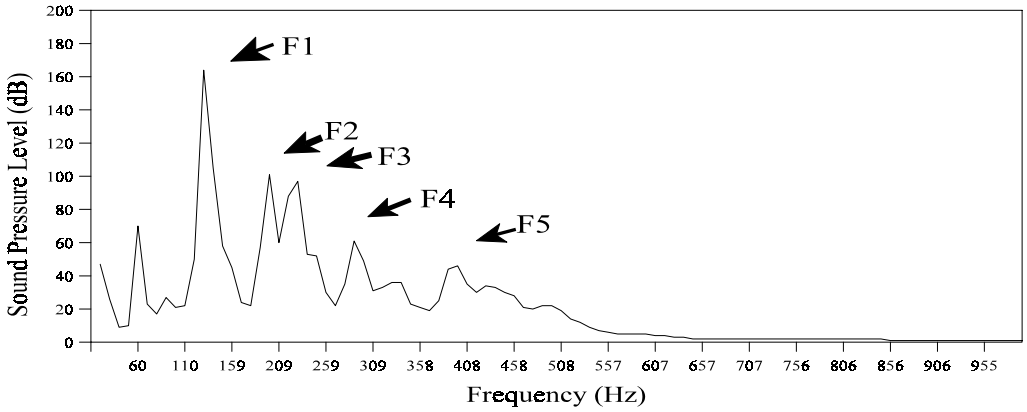

Figure 4. Wavelet derived power spectrum from *Lepomis megalotis* courtship pulse in Figure 7. F1-F5 indicate frequency peaks. F1 is the dominant frequency. Processing parameters: 11025 sampling rate, 100 frequency bins, 1000 Hz maximum threshold, -0.15 damping rate.

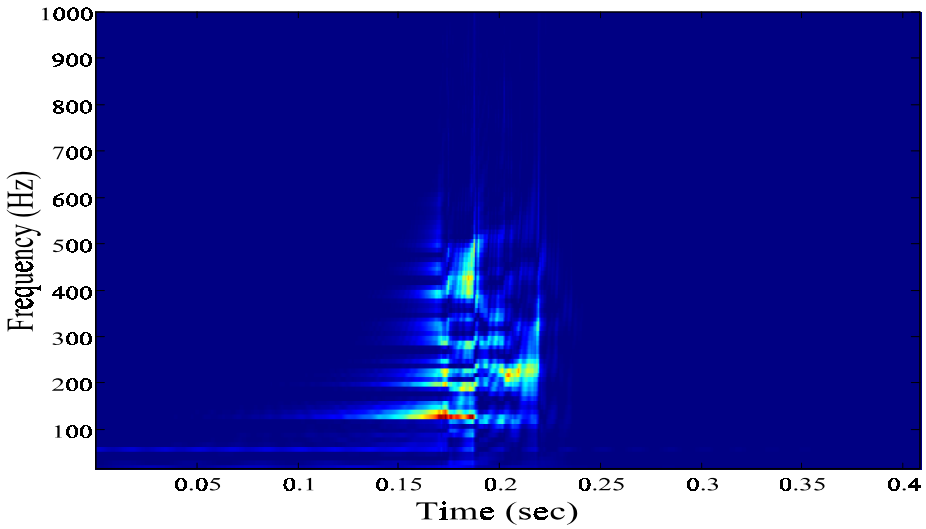

Figure 5. Wavelet derived spectrogram of *Lepomis megalotis* courtship pulse in Figure 7. Processing parameters: 11025 sampling rate, 100 frequency bins, maximum threshold 1000 Hz, wavelet damping rate -0.15. Color indicates intensity with blue indicating no intensity and red indicating highest intensity.

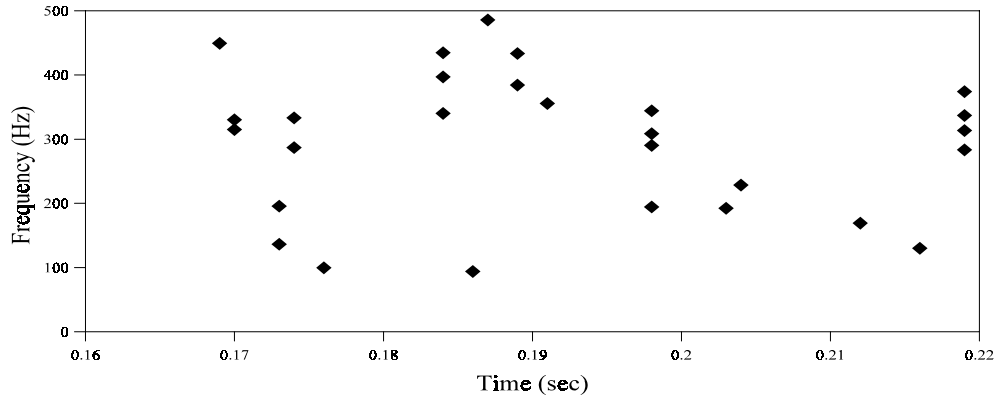

Figure 6. Modes derived from the wavelet spectrogram in Figure 5. See Table 3 for details associated with each mode. A mode is basically a localized energy peak. Note the difference in time and frequency scale between figures.

	Time (sec)	Duration (msec)	Center Frequency (Hz)	Decay Rate	Relative Energy
	0.170	5	315	-48	0.04
F1	0.173	38	136	-23	1.00
	0.173	21	196	-31	0.28
	0.174	15	287	-34	0.19
	0.184	3	397	-166	0.25
	0.187	4	486	-161	0.15
	0.189	3	384	-159	0.05
	0.198	4	290	-98	0.10
	0.198	4	344	-92	0.05
	0.203	15	192	-26	0.13
F2	0.204	15	229	-47	0.91
	0.219	1	283	-399	0.06

Table 3. Details associated with the modes derived from wavelet analysis. The modes are plotted in Figure 6 and spectrogram in Figure 5. F1 = dominant frequency, F2 = second frequency. Only modes > 0.03 energy are listed.

Temporal information was extracted from the waveform for the Fourier analysis (Figure 7), while it was extracted from the modes for the wavelet analysis. Figure 7 illustrates where pulse duration, rise time, and fall time were measured from the waveform. Pulse duration was calculated from modes by subtracting the peak time of the first mode from the last mode in a pulse or the duration of the longest mode, whichever was greater. Rise time was calculated using the first mode and peak mode (mode with highest energy), while fall time was based on peak mode and last mode.

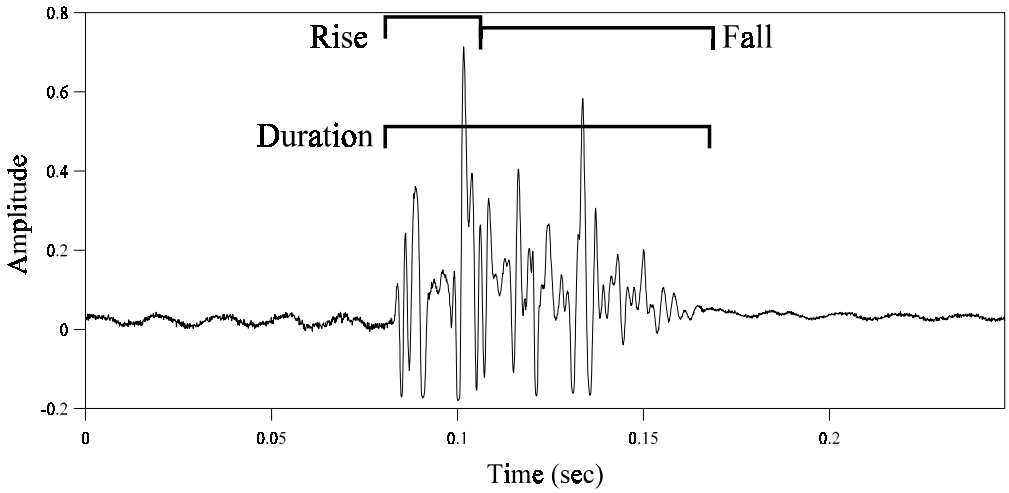

Figure 7. Waveform of *Lepomis megalotis* courtship pulse with labeled temporal parameters.

The output was grouped into three analysis methods: Fourier power spectra, wavelet power spectra, and wavelet modes. For synthetic calls, results were summarized by calculating the difference between the frequency determined by the analysis and actual frequency programmed. To normalize the data, these differences were log transformed (Zar 1999). Analysis of variance (ANOVA) was used initially to determine if there were any differences among the analysis methods. Paired t-tests compared the analysis methods to determine whether Fourier results were different than either of the wavelet methods and whether the two wavelet methods were different from each other. Post-hoc analyses using ANOVA were performed to assess whether signal type (sine or gaussian), dominant frequency (55 or 507 Hz) or duration affected the differences within a given analysis method.

RESULTS

Synthetic Calls

The first step to compare Fourier and wavelet transforms was to generate synthetic signals of known frequency and temporal composition. None of analyses (Fourier power spectra, wavelet power spectra, wavelet modes) yielded dominant frequencies (F1) that were significantly different than the programmed F1 (paired t-

test, min p = 0.36). Fourier data consistently had the greatest F1 and F1+F2 differences, while wavelet data had smaller F1 and F1+F2 differences (Table 4).

	F1 Difference (Hz)		F1 + F2 Difference (Hz)	
Analysis	**Mean**	**Max**	**Mean**	**Max**
Fourier Spectra	4.6	44.2	11.9	99.0
Wavelet Spectra	2.8	19.7	7.8	56.5
Wavelet Modes	2.2	27.6	8.7	73.6

Table 4. Summary of differences between programmed frequencies and analyzed frequencies. Mean indicates the average difference between the frequency determine from the analysis and the programmed frequency, while Max indicates the maximum difference observed for that method.

Overall, analysis method did affect the difference between the dominant frequency calculated by the analysis and that programmed (ANOVA, n = 20 calls, F = 5.16, p = 0.01) and the summed differences for the dominant and second frequencies (ANOVA, n = 20 calls, F = 3.31, p = 0.05). There were no differences among analysis methods based on signal type (ANOVA, min p = 0.49), but there were differences based on duration (ANOVA, max p = 0.009).

Analysis methods were compared more explicitly using paired t-tests. Fourier power spectra results were significantly different from wavelet modes for F1 (paired t-test, Bonferroni p = 0.01). Wavelet mode and wavelet power spectra results indicated differences but only before correction (paired t-test, p = 0.04,

Bonferroni p = 0.10). Fourier power spectra and wavelet power spectra results were not significantly different in any of the comparisons (paired t-tests, min p = 0.22).

To further explore differences within each analysis method, the different parameters were analyzed to see which ones affected which analysis method (ANOVA results in Table 5). Using only the difference in F1, signal type (sine or gaussian) did not affect any of the analyses (ANOVA, min p = 0.44). Duration affected Fourier analysis (ANOVA, F = 4.01, p = 0.02), but not either of the wavelet analyses (ANOVA, min p = 0.15). Dominant frequency (55 or 507 Hz) affected the wavelet power spectra analysis (ANOVA, F = 6.85, p = 0.02) but not Fourier power spectra or wavelet modes (ANOVA, min p = 0.29). Using the sum of the differences for F1 and F2, neither dominant frequency or signal type affected any analyses (ANOVA, min p = 0.25). Duration affected both Fourier analysis (ANOVA, p < 0.001) and wavelet power spectra analysis (ANOVA, p < 0.001), but not wavelet modes (ANOVA, p = 0.09).

	F1 Difference			F1 + F2 Difference		
Analysis	**Signal**	**F1**	**Duration**	**Signal**	**F1**	**Duration**
Fourier Spectra	n.s.	n.s.	p = 0.02	n.s.	n.s.	p < 0.001
Wavelet Spectra	n.s.	p = 0.02	n.s.	n.s.	n.s.	p < 0.001
Wavelet Modes	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.

Table 5. Summary of exploratory ANOVA results. F1 = dominant frequency. n.s. = non-significant.

While all methods recovered the two predominant frequencies (55 Hz and 507 Hz), all methods occasionally missed one of the other three frequencies (123, 203 or 1110 Hz). Fourier analysis dropped 6 frequencies out of a potential 60 misses for those three frequencies over 20 signals. Wavelet power spectrum analysis dropped 13 frequencies, while wavelet modal analysis dropped 27 frequencies. The number of frequencies dropped by wavelet modes could be adjusted by lowering the threshold used to select the modes. In addition, adjusting the damping rate of the wavelet or type of wavelet can also reduce the number of frequencies dropped. There are a number of protocols for and discussions about selecting the type of wavelet and damping rate (e.g. Senhadji et al. 1995). Overall, Fourier power spectra yielded the greatest overall differences between programmed frequencies and analyzed frequencies, even though wavelets dropped more the frequencies (which can optimized by adjusting threshold and wavelet type).

Real Calls

All three analysis methods, Fourier, wavelet power spectra, and wavelet modes, were used to analyze a set of calls from a variety of animals, including a cricket, fishes and frogs. Since there is no way to compare each method to an objective standard, the dominant (F1) and second (F2) frequencies as determined by each method are presented in Tables 6 - 9. To facilitate reading the tables and applying to later chapters, longear sunfish (*Lepomis megalotis*) calls are presently separately (Tables 6 -7) from the other taxa (Tables 8 - 9)

For longear sunfish calls, there were more discrepancies among the pursuit calls than the courtship calls and in the second frequency than the dominant frequency. This was also true for all the other taxa. The discrepancies for all fish, except *Cyprinella* and *Lepomis*, were less than 10 Hz for dominant frequency. For the remaining taxa, discrepancies were of much greater magnitude, as much 170 Hz for *Acris crepitans*. The magnitude of the discrepancies was also greater for the second frequency than the dominant frequency for all taxa. There were more and larger discrepancies for longear sunfish and *Cyprinella* calls, which had the least tonal quality of all calls, than any other taxa, .

Taxon and Call Type	Fourier Power Spectra	Wavelet Power Spectra	Wavelet Modes
Lepomis megalotis courtship pulse	333.8	331.8	329.5
Lepomis megalotis courtship pulse	226.1	128.8	136.4
Lepomis megalotis courtship pulse	172.3	173.4	172.8
Lepomis megalotis courtship pulse	129.2	143.7	141.7
Lepomis megalotis pursuit pulse	96.9	104.1	102.5
Lepomis megalotis pursuit pulse	150.7	418.3	148.6
Lepomis megalotis pursuit pulse	64.6	59.6	57.4
Lepomis megalotis pursuit pulse	86.1	89.3	93.8

Table 6. Dominant frequency for pulses from *Lepomis megalotis* as determined by each of the three analyses. Wavelet damping rate = -0.15 with 200 frequency bins.

Taxon and Call Type	Fourier Power Spectra	Wavelet Power Spectra	Wavelet Modes
Lepomis megalotis courtship pulse	387.6	123.9	382.6
Lepomis megalotis courtship pulse	118.4	222.9	231.3
Lepomis megalotis courtship pulse	97.0	94.2	339.0
Lepomis megalotis courtship pulse	215.3	178.3	184.9
Lepomis megalotis pursuit pulse	204.6	64.5	158.2
Lepomis megalotis pursuit pulse	96.9	94.2	418.3
Lepomis megalotis pursuit pulse	183.0	44.7	204.9
Lepomis megalotis pursuit pulse	183.0	149.8	59.6

Table 7. Second frequency for pulses from *Lepomis megalotis* as determined by each of the three analyses. Wavelet damping rate = -0.15 with 200 frequency bins.

Taxon and Call Type	Fourier Power Spectra	Wavelet Power Spectra	Wavelet Modes
Cyprinodon bifasciatus	193.8	194.1	195.8
Cyprinodon bifasciatus	247.6	246.3	247.9
Cyprinodon bifasciatus	721.4	723.9	718.9
Pimephales notatus moan*	172.3	168.4	172.1
Pimephales notatus drum	172.3	168.4	167.6
Pimephales notatus moan*	140.0	138.7	141.3
Pimephales notatus drum	129.2	123.9	124.4
Pimephales notatus knock	129.2	123.9	122.6
Etheostoma crossoptera moan*	140.0	138.7	141.4
Etheostoma crossoptera knock	161.5	165.8	163.5
Etheostoma crossoptera moan*	172.3	178.3	183.7
Etheostoma nigripinne knock	107.7	104.6	104.7
Etheostoma nigripinne knock	107.7	109.1	107.1
Etheostoma nigripinne moan*	150.7	148.6	158.0
Cyprinella venusta one pulse	398.4	99.2	99.4
Cyprinella venusta one pulse	452.2	450.6	112.6
Gryllus integer one pulse	5491.0	5534.4	5492.3
Acris crepitans one pulse group	3531.5	3432.0	3434.0
Acris crepitans one pulse group	3488.4	3432.0	3310.0
Hyla cinerea one pulse^{+}	3100.8	3130.9	3115.0
Hyla cinerea one pulse^{+}	3100.8	3130.9	3125.3
O. americanus one pulse^{+}	818.3	825.8	825.1

Table 8. Dominant frequency, as determined by each analysis, for pulses from a variety of taxa (See Methods for more details). * indicates calls analyzed with a wavelet damping rate of -0.40 instead of -0.15. $^{+}$ indicates calls analyzed with a wavelet damping rate of -0.05 instead of -0.15.

Taxa	Fourier Power Spectra	Wavelet Power Spectra	Wavelet Modes
Cyprinodon bifasciatus	290.7	298.6	297.3
Cyprinodon bifasciatus	258.4	164.3	168.0
Cyprinodon bifasciatus	786.0	791.1	799.8
Pimephales notatus moan*	96.9	94.2	97.3
Pimephales notatus drum	161.5	89.3	136.6
Pimephales notatus moan*	290.7	74.4	84.9
Pimephales notatus drum	64.6	166.3	292.2
Pimephales notatus drum	290.7	292.2	291.3
Etheostoma crossoptera moan*	215.3	212.0	213.0
Etheostoma crossoptera knock	183.0	118.9	198.6
Etheostoma crossoptera moan*	538.3	--	187.6
Etheostoma nigripinne knock	215.3	59.6	--
Etheostoma nigripinne knock	172.3	24.9	23.3
Etheostoma nigripinne moan*	96.9	24.9	102.9
Cyprinella venusta one pulse	96.9	198.1	388.2
Cyprinella venusta one pulse	86.1	440.7	486.7
Gryllus integer one pulse[#]	--	--	--
Acris crepitans one pulse group	5254.1	5238.3	5305.0
Acris crepitans one pulse group	5383.3	5288.5	5225.0
Hyla cinerea one pulse[+]	947.5	2829.9	2850.6
Hyla cinerea one pulse[+]	947.5	2829.9	2858.0
O. americanus one pulse[+]	1550.4	722.5	722.5

Table 9. Second frequency, as determined by each analysis, for pulses from a variety of taxa (See Methods for more details). * indicates calls analyzed with a wavelet damping rate of -0.40 instead of -0.15. [+] indicates calls analyzed with a wavelet damping rate of -0.05 instead of -0.15. [#] *G. integer* calls had only one mode per pulse.

In addition, Figures 8 - 14 present comparisons of the output from Fourier and wavelet analyses, and are accompanied by the modal output in Tables 10 - 16, respectively. These figures and accompanying tables provide a graphical depiction of the difference in output and resolution among analysis methods. The quality of the spectrograms can be affected by analysis parameters.

Figure 8 is a longear sunfish, *Lepomis megalotis* (Centrarchidae), courtship call with four pulses from a parental male (See Figure 17 for another courtship call and Figure 19 for a pursuit call in Chapter 3). It is unknown how the sound is produced, but it is a low frequency, broad band, non-harmonic sound (See Gerald (1970; 1971) for the original description and Chapter 3 for more detail). Modes from the wavelet analysis are presented in Table 10.

Pulse	Time (sec)	Duration (msec)	Center Frequency (Hz)	Decay Rate	Relative Energy
1	0.150	11	245.6	-39	0.11
1	0.151	8	181.9	-41	0.04
2	0.376	25	168.9	-13	0.06
3	0.581	2	339.4	-175	0.05
3	0.581	1	498.7	-196	0.03
3	0.593	24	171.2	-44	0.68
3	0.593	1	261.9	-238	0.02
4	0.890	25	153.9	-45	1.00

Table 10. Modes extracted from wavelet analysis in Figure 8 for *Lepomis megalotis*. Only modes with a relative energy > 0.01 have been included.

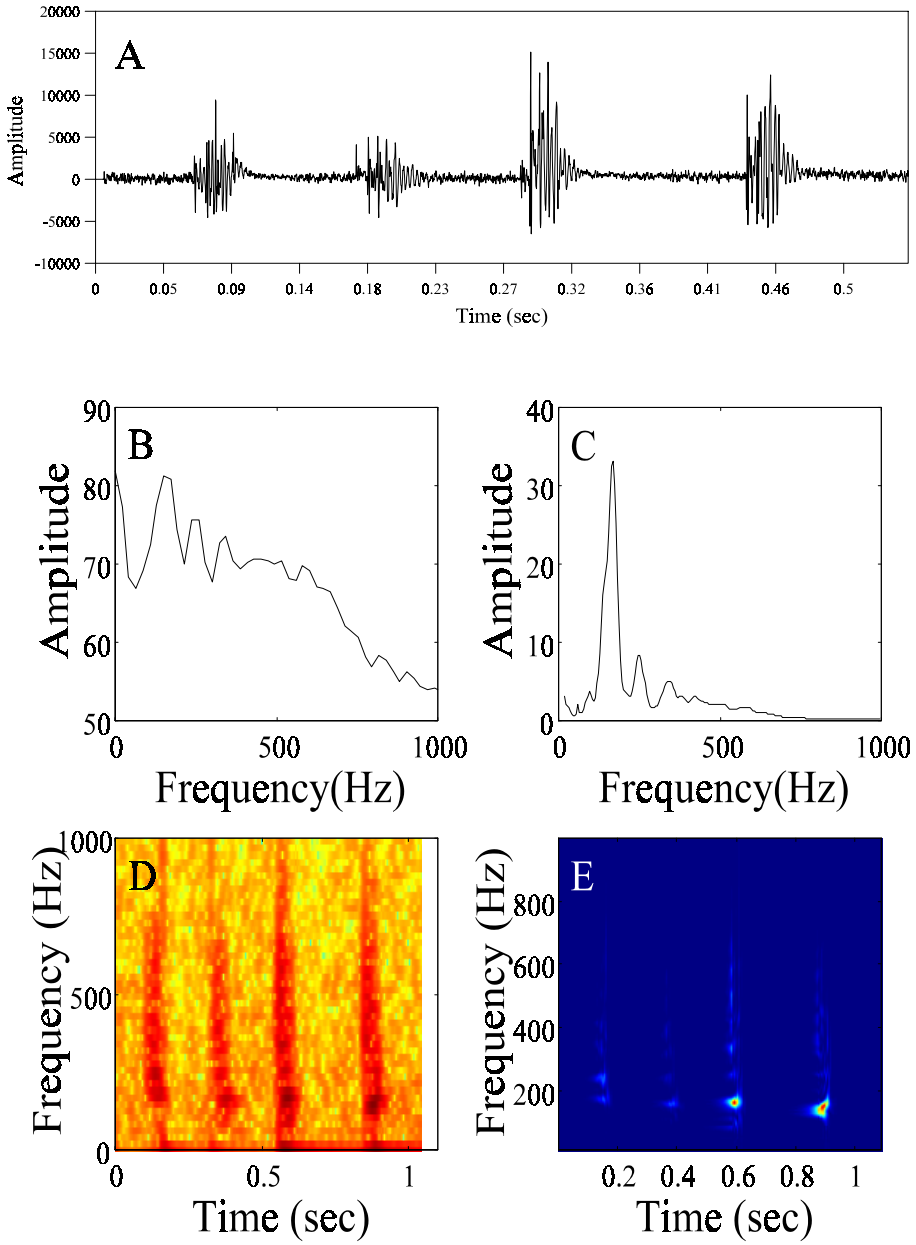

Figure 8. Longear sunfish (*Lepomis megalotis*) courtship call with a comparison of output from Fourier (B,D) and wavelet (C,E) analysis. A is oscillogram. B,C, are power spectra and D,E are spectrograms.

Figure 9 is a two-line pupfish, *Cyprinodon bifasciatus* (Cyprinodontidae), call from a territorial male. It is unknown how the sound is produced, but it is a low frequency, broad band, non-harmonic sound produced by territorial parental males during reproduction (Johnson 2000). Modes from the wavelet analysis are presented in Table 11.

Time (sec)	Duration (msec)	Center Frequency (Hz)	Decay Rate	Relative Energy
0.115	36	297.9	-25	1.00
0.120	3	500.7	-93	0.03
0.127	37	196.0	-23	0.84
0.132	2	506.8	-101	0.02
0.137	0.5	703.7	-397	0.02
0.140	2	814.9	-45	0.02
0.148	5	394.8	-101	0.24
0.148	3	470.8	-93	0.02
0.148	3	675.8	-92	0.03
0.148	3	697.5	-103	0.03
0.149	3	777.2	-132	0.06
0.149	3	804.0	-120	0.03
0.156	2	302.8	-82	0.04
0.158	2	376.7	-146	0.03
0.159	5	444.5	-73	0.03
0.161	2	462.8	-141	0.03

Table 11. Modes extracted from wavelet analysis in Figure 9 for *Cyprinodon bifasciatus*. Only modes with a relative energy > 0.01 have been included.

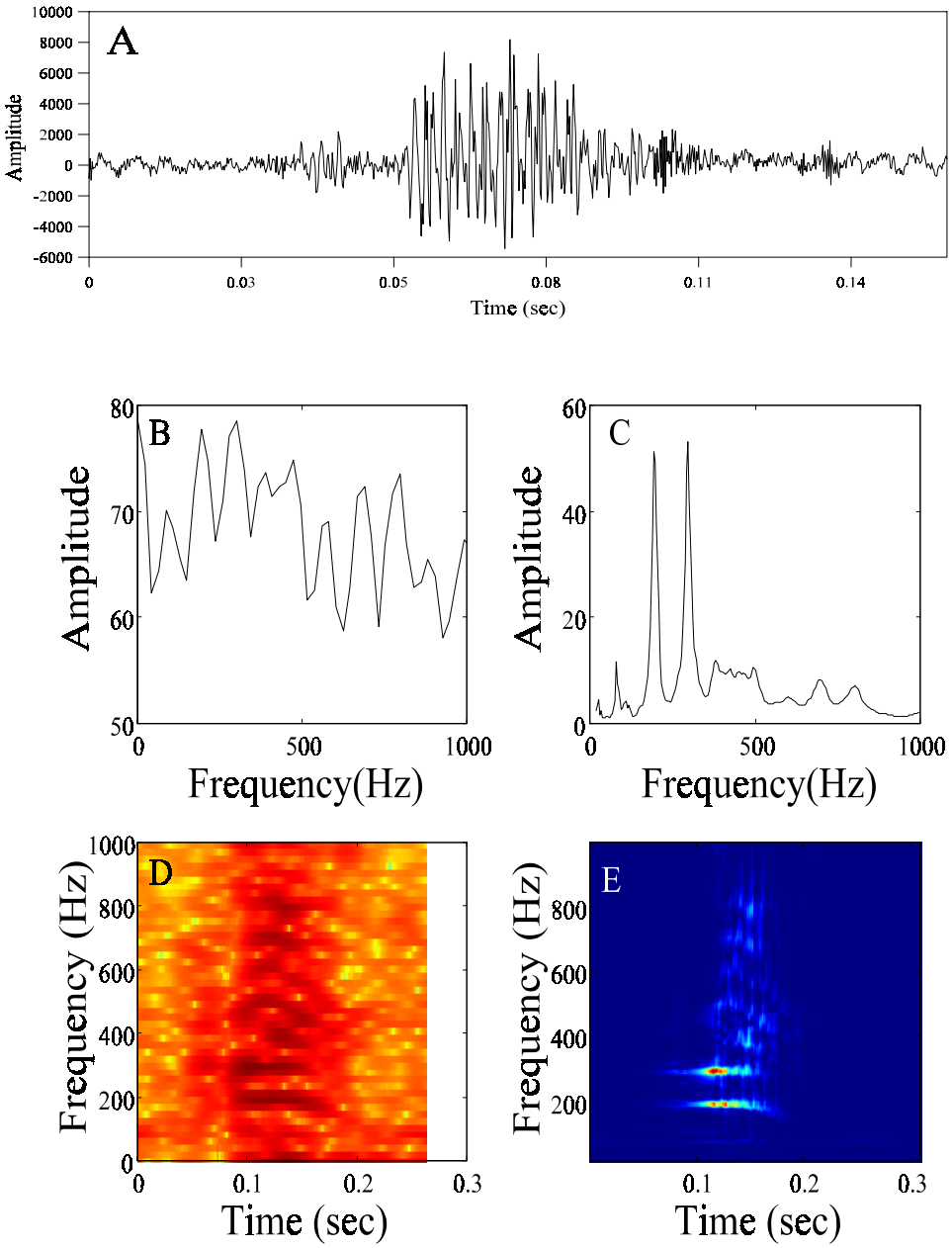

Figure 9. Twoline pupfish (*Cyprinodon bifasciatus*) territorial male call with comparison of Fourier (B,D) and wavelet (C,E) analyses. A is the oscillogram, B and C are power spectra and D and E are spectrograms.

Figure 10 is a fringed darter, *Etheostoma crossoptera* (Percidae), call from a territorial male. It is unknown how the sound is produced, but calls are composed of multiple components of low frequency, including moans and knocks (Johnston & Johnson 2000a). This call is a moan followed by two knocks. Modes were extracted from the wavelet analysis and are presented in Table 12.

Pulse	Time (sec)	Duration (msec)	Center Frequency (Hz)	Decay Rate	Relative Energy
1	0.228	31	210.3	-26	0.11
1	0.465	225	141.7	-5	1.00
2	1.401	49	165.4	-19	0.14
3	1.841	10	200.3	-23	0.02
3	1.860	43	166.8	-17	0.07

Table 12. Modes extracted from wavelet analysis in Figure 10 for *Etheostoma crossoptera*. Only modes with a relative energy > 0.01 have been included.

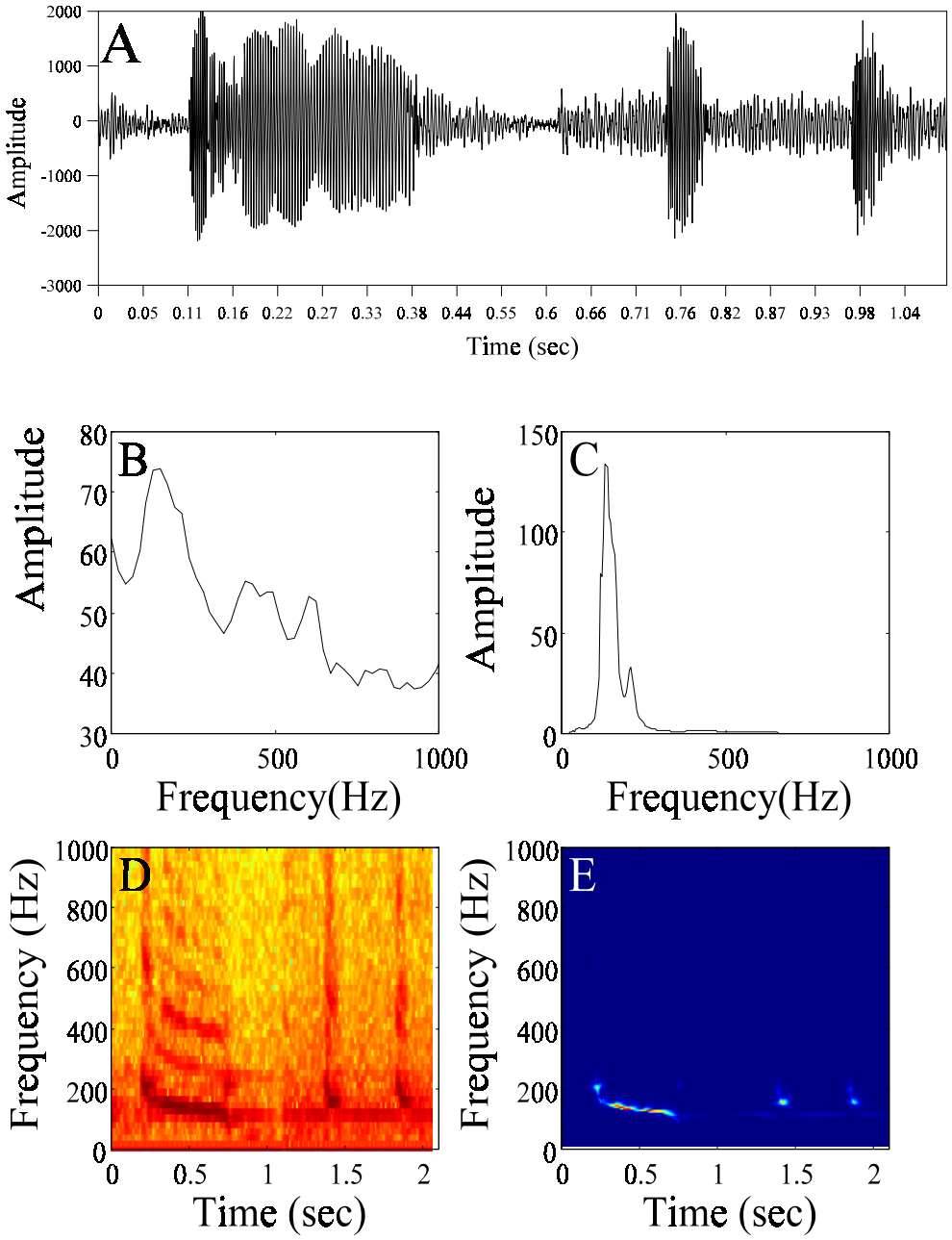

Figure 10. Fringed darter (*Etheostoma crossoptera*) call from a reproductive male with comparison of Fourier (B, D) and wavelet (C, E) analyses. A is an oscillogram, B and C are power spectra and D and E are spectrograms.

Figure 11 is a bluntnose minnow, *Pimephales notatus* (Cyprinidae), call from a territorial male. It is unknown how the sound is produced, but the calls are composed of multiple components of low frequency sounds including moans, drums and knocks (Johnston & Johnson 2000b). This call is a moan and four knocks. Modes were extracted from the wavelet analysis and are presented in Table 13.

Pulse	Time (sec)	Duration (msec)	Center Frequency (Hz)	Decay Rate	Relative Energy
1	0.099	147	103.3	-58	1.00
1	0.111	63	121.1	-27	0.30
1	0.120	7	122.7	-31	0.02
1	0.156	18	123.9	-21	0.03
2	0.321	6	140.4	-27	0.02
2	0.322	14	143.7	-71	0.05
3	0.473	28	143.7	-11	0.08
4	0.647	4	168.0	-26	0.02
4	0.651	31	168.5	-15	0.14
5	0.839	25	227.4	-136	0.10

Table 13. Modes extracted from wavelet analysis in Figure 11 for *Pimephales notatus*. Only modes with a relative energy > 0.01 have been included.

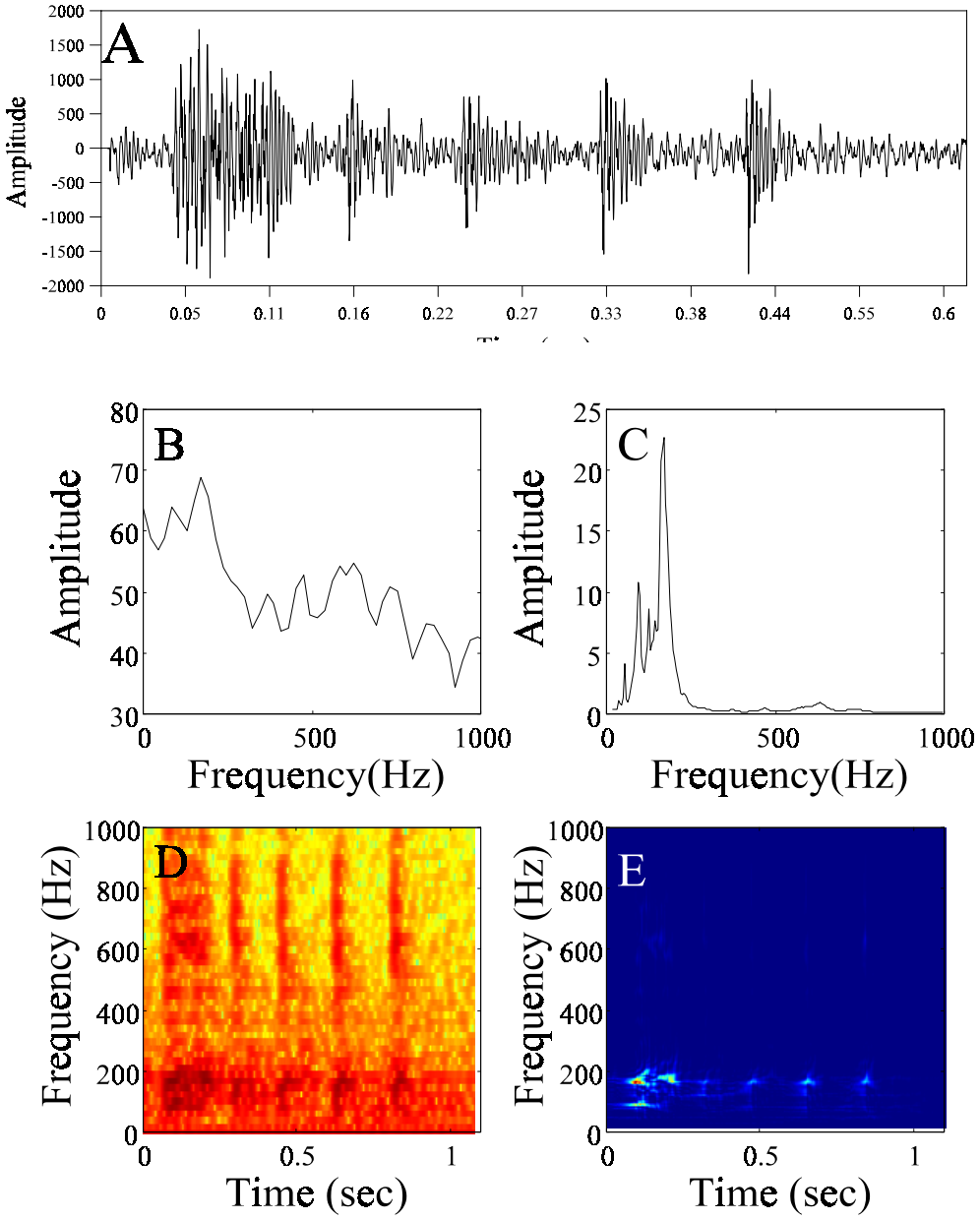

Figure 11. Bluntnose minnow (*Pimephales notatus*) call from a male with comparison of Fourier (B, D) and wavelet (C, E) analyses. A is an oscillogram, B and C are power spectra and D and E are spectrograms.

Figure 12 is a cricket frog, *Acris crepitans* (Hylidae), call from a male. The call consists of a series of pulses (in pulse groups) with a sideband structure (Ryan & Wilczynski 1991; Wagner 1991). Modes were extracted from the wavelet analysis and are presented in Table 14.

Pulse	Time (sec)	Duration (sec)	Center Frequency (Hz)	Decay Rate	Relative Energy
1	0.014	0.5	5211.5	-1751	0.05
1	0.015	1	3290.1	-712	0.94
2	0.035	0.5	5488.4	-1527	0.14
2	0.036	0.5	5407.2	-1768	0.13
2	0.036	1	3437.8	-674	1.00
3	0.041	0.5	5416.8	-2086	0.11
3	0.042	0.5	5314.7	-627	0.09
3	0.042	1	3473.0	-830	0.99
4	0.047	0.5	5356.2	-2017	0.09
4	0.048	0.5	5311.5	-329	0.07
4	0.048	1	3503.6	-1045	0.84
5	0.053	0.5	5405.5	-1163	0.06
5	0.054	0.5	5286.9	-1107	0.06
5	0.054	1	3507.3	-1032	0.67

Table 14. Modes extracted from wavelet analysis in Figure 12 for *Acris crepitans*. Only modes from the first five pulses are included.

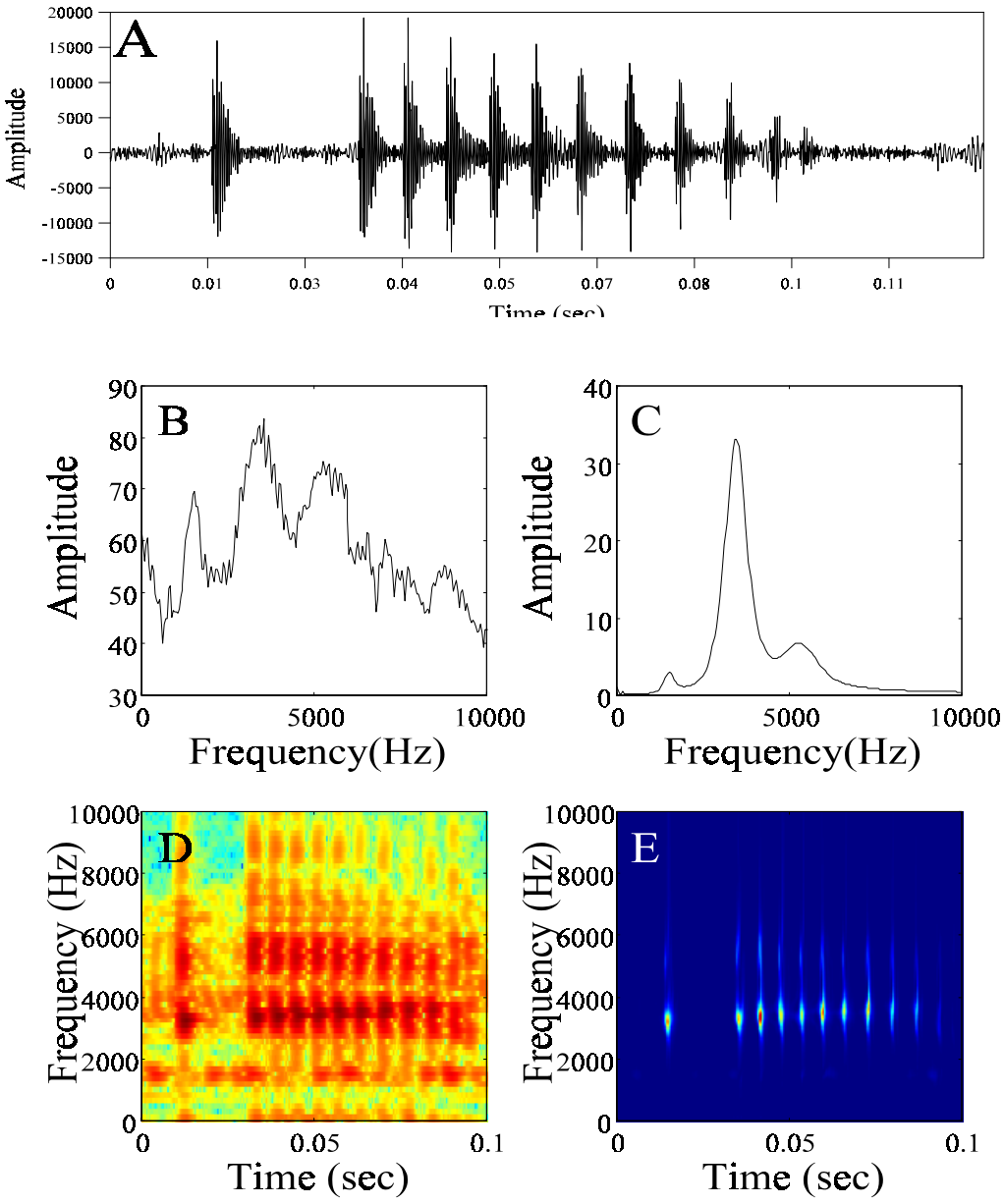

Figure 12. Cricket frog (*Acris crepitans*) call from a male with comparison of the Fourier (B,D) and wavelet (C,E) analyses. A is an oscillogram, B and C are power spectra and D and E are spectrograms.

Figure 13 is a green tree frog, *Hyla cinerea* (Hylidae), call from a male (Gerhardt & Klump 1988). The call is a short frequency sweep. Modes were extracted from the wavelet analysis and are presented in Table 15.

Time (sec)	Duration (msec)	Center Frequency (Hz)	Decay Rate	Relative Energy
0.094	17	2850.0	-44	0.16
0.113	55	3115.0	-21	1.00
0.132	23	923.2	-10	0.06

Table 15. Modes extracted from wavelet analysis in Figure 13 for *Hyla cinerea*. Only modes with a relative energy > 0.01 have been included.

Figure 14 is a field cricket, *Gryllus integer* (Gryllidae), call from a male. This is a pulsed call produced by and generates a series of short pulses in rapid succession for long time periods (Alexander 1962; Stephen & Hartley 1995). Modes were extracted from the wavelet analysis and are presented in Table 16.

Pulse	Time (sec)	Duration (msec)	Center Frequency (Hz)	Decay Rate	Relative Energy
1	0.005	3	5561.0	-195	0.93
2	0.015	2	5497.4	-222	0.89
3	0.025	3	5544.0	-235	1.00
4	0.036	2	5590.5	-279	0.98
5	0.047	2	5547.5	-236	0.89
6	0.057	2	5483.6	-212	0.72

Table 16. Modes extracted from wavelet analysis in Figure 14 for *Gryllus integer*. Only modes with a relative energy > 0.01 have been included.

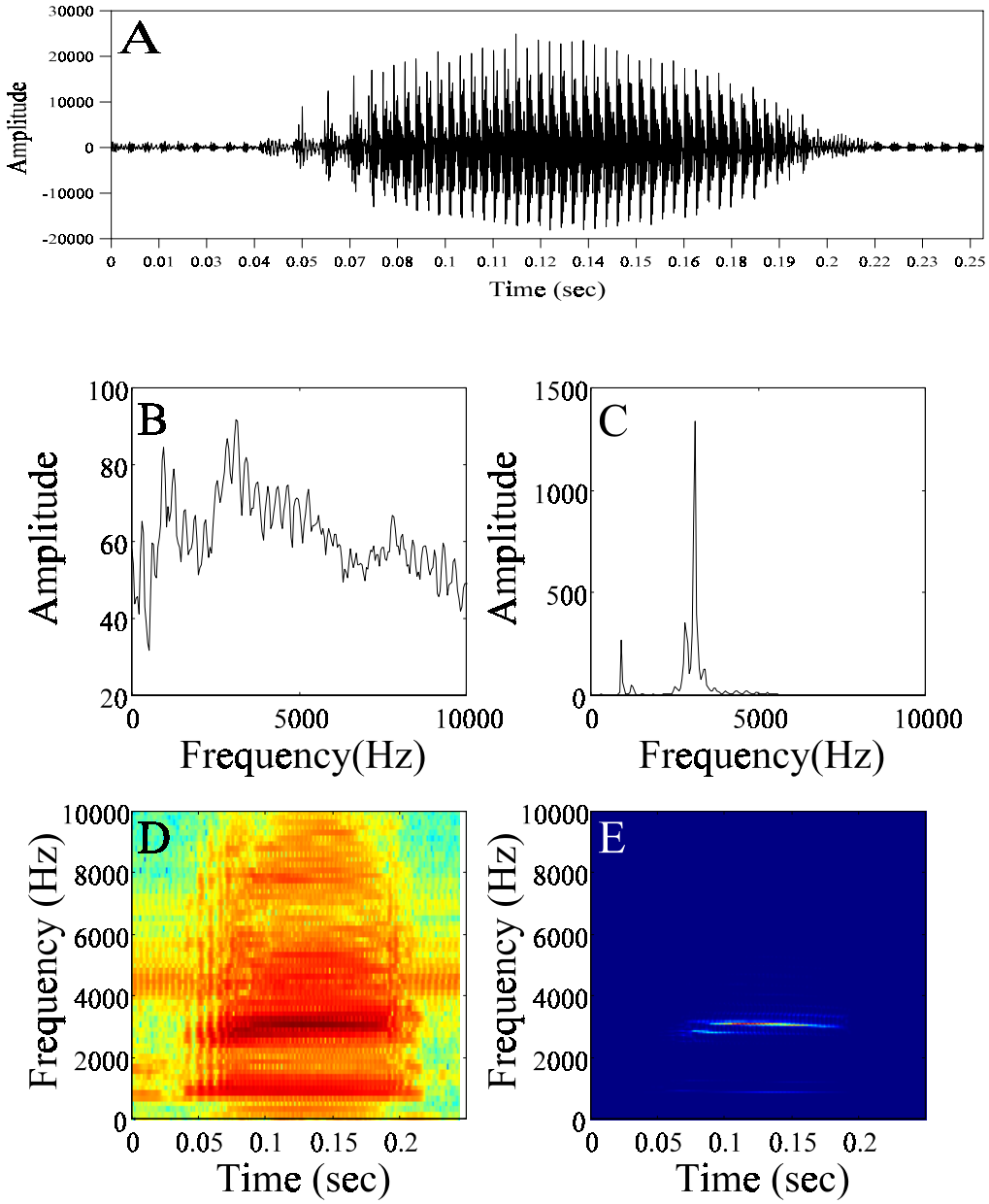

Figure 13. Green tree frog (*Hyla cinerea*) call from a male with a comparison of the Fourier (B, D) and the wavelet (C, E) analysis. A is an oscillogram, Band C are power spectra, and D and E are spectrograms.

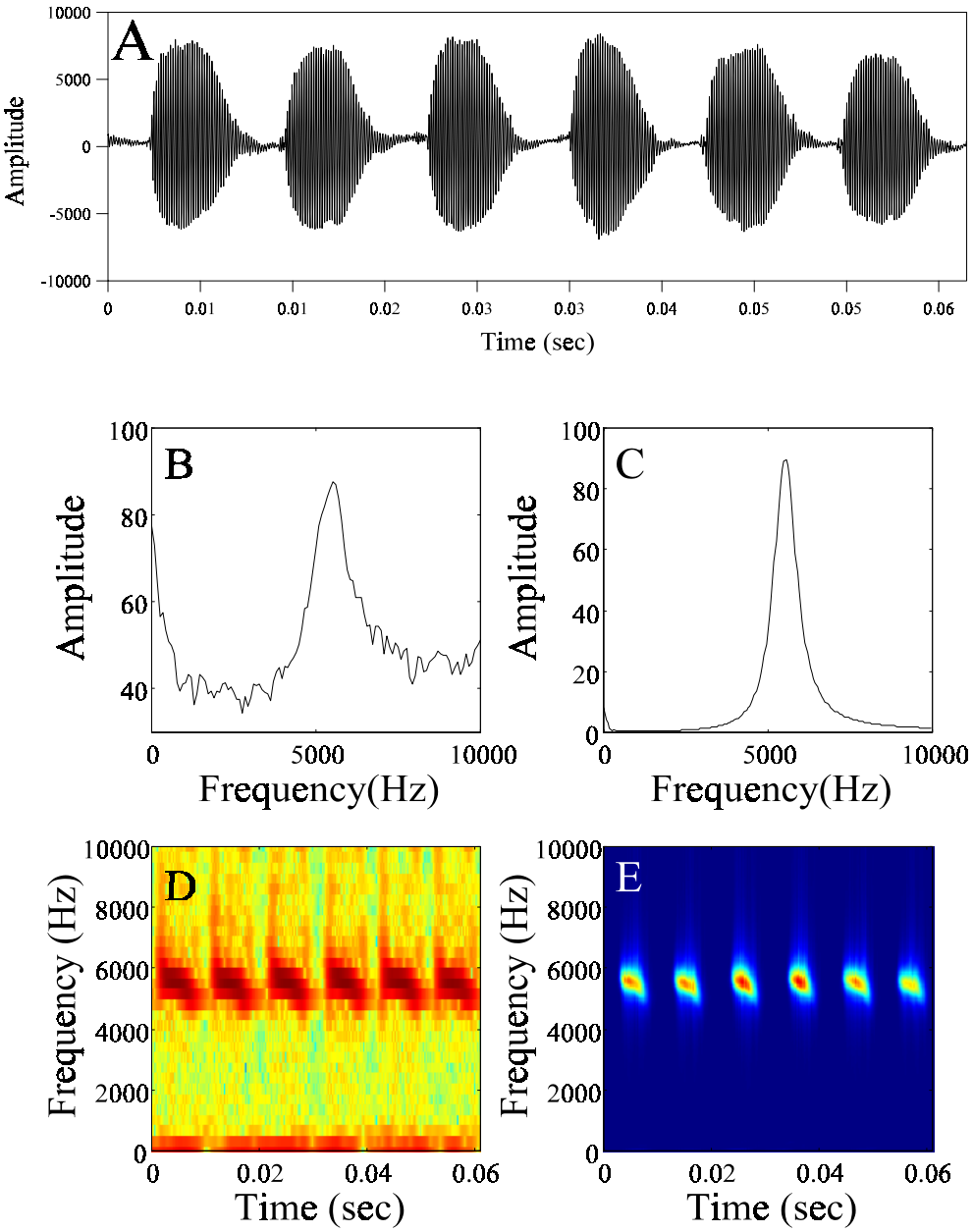

Figure 14. Field cricket (*Gryllus integer*) call with a comparison of the Fourier (B, D) and wavelet (C, E) analysis. A is an oscillogram, B and C are power spectra, and D and E are spectrograms.

DISCUSSION

Signals that will benefit most from the use of wavelet transforms generally take the form of broad band, short duration and low frequency signals, as seen in *Lepomis megalotis* and *Pimephales notatus*. Additionally, the short pulse durations seen in *Gryllus integer* and *Acris crepitans* benefit from the accuracy of wavelets and the modal information extracted from wavelets, with each pulse being thoroughly characterized. The graphical depiction of the Fourier spectrogram can be affected by the exact settings used, but even with an optimal depiction of the Fourier spectrogram it is less clean than the wavelet spectrogram. While, not all spectral analyses are created equal, they are all subject to a certain amount of error as they are all estimates of the frequency information present in a signal.

There are calls for which the benefit of wavelets is not substantial. Calls of high frequency with relatively long durations can be analyzed with good resolution using traditional Fourier transforms and do not require investment in new software. Many bird songs and a portion of frog calls fall in this category. Wavelets can still be a useful tool, but the discrepancies are smaller. Table 17 provides some duration and frequency guidelines to take into consideration. As a rule of thumb, a call with a duration less than 50 times the period is a prime candidate for, and would benefit the most from, the use of wavelet transforms. It is important to keep in mind that although these are guidelines for the dominant frequency, they become less relevant

for broad band calls that have frequencies that span a wide range. The dominant frequency may be resolved well, but lower frequencies may be poorly analyzed.

Frequency (Hz)	Period (msec)	50x (msec)
10	100	5000
50	20	1000
100	10	500
150	7	335
200	5	250
250	4	200
300	3	165
400	3	125
500	2	100
750	1	65
1000	1	50
1250	0.80	40
1500	0.67	33.5

Table 17. Suggested cutoff durations for considering wavelet analysis. The period of the waveform is indicated in the middle column. If a signal is less than 50x the period, the signal is a prime candidate for analysis using wavelet transforms.

In addition to the increased resolution as illustrated in the extensive figures, there are some additional advantages to using wavelets, as well as some limitations. As mentioned in the Introduction, the specificity of the wavelet actually results in some automatic filtering during processing. In other words, signals that do not match the wavelet are essentially ignored. The essentially infinite flexibility of

wavelets allows the user to analyze a wide variety of signals using the same techniques and still obtain high resolution by customizing the wavelet for each signal type. Computational time has historically been a limitation in wavelet analysis, but with increased computer speed this limitation has become negligible.

Time measurements can be calculated based on first and last mode in a pulse. This measurement provides a consistent underestimate of the duration compared to traditional time measurements based on waveform. However, it ignores any noise that can affect measurements based on waveforms. Noise can be particularly troublesome for low frequency calls in high noise environments, where the call is embedded in the noise. The many advantages of wavelets and the increased resolution provided by wavelets, as well as the increased information provided by modal extraction, substantially increase the data available for characterizing a signal and help understand the production mechanism.

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Chapter 3
Acoustic Behavior of Longear Sunfish
(Lepomis megalotis aquilensis)

Acoustic communication during reproductive behavior of longear sunfish (*Lepomis megalotis aquilensis*) in central Texas was studied using in-stream observations and underwater video and hydrophone recordings. Longear sunfish males produce both courtship and pursuit calls while nesting. Courtship calls are directed toward females and are given in conjunction with a distinctive visual courtship display. Females typically either enter the nest or are already in the nest when courtship calls are given. Pursuit calls are typically directed toward 'raiders' and are given during pursuits. Raiders typically respond to pursuit calls by either swimming away from the nest or changing course to avoid the nest. Courtship and pursuit calls produced by the same male differ in mean frequency and rise time. The amount of variation in pulse rate and frequency differs between contexts, with pursuit calls exhibiting more variation. Pursuit calls, like a combination of distress and release calls in frogs, are used with both conspecifics and heterospecifics and play a role in territory defense. Courtship calls, like advertisement calls in frogs, are used with females selecting mates and likely play a role in mate choice.

INTRODUCTION

The substantial body of research on acoustic communication in terrestrial organisms has led to a growing body of theory and conceptual understanding of how communication systems evolve and the mechanisms by which they operate (e.g. Hauser 1996; Kroodsma & Miller 1996; Ryan 2001). Acoustic communication in aquatic organisms, however, has not been as well studied. The types of calls made by marine mammals have been documented but studies clearly demonstrating function and how they are used in the wild are minimal (Berta & Sumich 1999; Richardson et al. 1995; Thomas et al. 1992). While sound production has been documented in many marine fishes (e.g. Bright 1972; Fish & Mowbray 1970), experimental studies in the field have been limited to damselfish (Albrecht 1981; Lobel & Mann 1995; Mann & Lobel 1997; 1998; Myrberg 1997).

It is important to clearly describe the acoustic behavior of fishes in their natural setting before beginning detailed experimental research in the laboratory, yet few studies have done this. Previous work on sunfish (Gerald 1971), the description of sound production in *Cyprinodon bifasciatus* (Johnson 2000), and the acoustic behavior of the electric fish *Pollimyrus isidori* (Crawford et al. 1997) are the only published studies on freshwater fish sound production in the field. Invariably, animals are captured and held in glass or plexiglass aquaria and data collected are assumed to represent how the fish, and the sound, behave in the field

(e.g. Ladich 1989; Ladich & Kratochvil 1989; Rigley & Marshall 1973; Schwarz 1980; Stout 1975; Valinski & Rigley 1981). However, due to the unnatural setting and acoustic properties of aquaria, signals may be distorted or made during contexts non-existent or infrequent in the field (Okumura et al. 2001).

Only two studies on acoustic behavior in sunfish have been published. The first was Gerald's (1971) initial description of sound production in *Lepomis* reporting calls during courtship activities in *L. megalotis*, *L. macrochirus*, *L. microlophus , L. humilis*, *L. punctatus* (now *L. miniatus* (Warren 1992)), and *L. cyanellus*, and lack of sound production in *L. auritus*. In all species, the majority of spectral energy is below 1000 Hz. Pulse duration ranged from 20 msec in *L. cyanellus* to over 200 msec in *L. humilis*. *L. megalotis* calls were described with a maximum frequency of 1300 Hz, average call duration of 65 msec and an average pulse rate of 72 pulses per second. Gerald (1970, 1971) concluded that sounds produced by different species varied sufficiently in duration and pulse rate to facilitate species recognition. The techniques available to Gerald limited frequency resolution, so conclusions regarding differences in dominant frequency were minimal. Prior to digital signal processing and high speed computers, analysis was limited to measuring the waveform and frequency peaks on a power spectrum (Littlejohn 1989). Gerald's study also had only limited descriptions of the behavior associated with sound production and only focused on courtship calls.

The second published study on sound production was a series of papers on hybrids of pumpkinseeds (*L. gibbosus)* and bluegill (*L. macrochirus*) conducted in wading pools and aquaria (Ballantyne & Colgan 1978a,b,c). Ballantyne and Colgan (1978a,b,c) concluded that acoustic signals were used to indicate transitions between aggressive and non-aggressive behavior and calls were directed to both conspecifics and heterospecifics. A few of their observations and many of their conclusions were in contrast to previous studies such as those by Miller (1963) and Keenleyside (1967) and with my own observations. The source of most of the discrepancies is the premise that sound production occurred during 'internal conflict' and transitions between different types of activity. The lack of signal analysis also resulted in some false interpretations. Ballantyne and Colgan (1978a,b,c) report that all sound production was associated with biting behavior, which was rare in the field, possibly because there were no aquaria walls to constrain retreats. It is particularly surprising that most sounds were associated with biting, when the majority of sound production in field observations occured during surfacing displays when the female was at a distance from the male, not during biting or chasing a female (see Results and Gerald 1970). Sounds produced from the physical contact during biting do not constitute a signal in terms of communication. Ballantyne and Colgan (1978a,b,c) did suggest that sound production was only one part of elaborate displays observed during courtship,

which also included visual, and possibly chemical, signals. They also suggested that responses to sound production were based more on a visual orientation toward the sender, which agrees with my (lack of) observations during acoustic playbacks. Overall, the lack of signal processing, confined laboratory situation and focus on 'transition' behavior led Ballantyne and Colgan to interpret their data in ways that do not agree with field observations and that can not be applied to in situ behavior.

The goal of this chapter is to characterize the acoustic communication system in *L. megalotis aquilensis* for both the sender and the receiver. This includes a detailed description of sender and receiver behavior during sound production, as well as a brief description of the hearing ability of longear sunfish. I will also present the structural differences between courtship and pursuit calls and speculate as to possible functions of these calls. For more information on variation in the signals, see Chapter 5.

MATERIALS AND METHODS

Nests of parental males were studied in clear, shallow streams in Austin, Texas from May to August in 1998, 1999, and 2000. Synchronized video and audio recordings were made on Hi-8 metal particle videotapes using a Benthos AQ-20 hydrophone plugged into the external microphone input of a Hitachi VMH-100LA videocamera. The submersible lens and hydrophone were placed on the edge of

the nest and recordings began when the male was acclimated, typically less than 15 minutes. Males were considered acclimated when they resumed patrol and defense activities. Body weight, using a Pesola™ scale, and fork length, from snout to fork in caudal tail, were measured in males captured in the field.

The terms 'parental male', 'sneaker', 'ripe female' and 'raider' will be used throughout this chapter to indicate discrete behavioral categories. A parental male is a large (100 - 125 mm SL at most sites) reproductive male with full colors that is defending a nest that may or may not already have offspring. A sneaker male (as used by Gross 1982) is a small (50 - 80 mm SL) reproductive male that 'sneaks' into a spawning event and attempts to fertilize eggs. A ripe female is a female that is actively performing mate selection, has changed color from the nondescript lavender tinted pattern typical of juveniles to a distinctive vertical striping, is likely excreting an olfactory cue and that will spawn within the next few hours (pers. obs.). A raider is any fish that attempts to enter the nest to eat eggs. Most raiders were conspecific juveniles, sneaker males, females, or even other parental males. Some raiders were other *Lepomis* species and it was often difficult to distinguish among juveniles and sneaker males of *Lepomis* in the field. Species from other genera also raided nests but were recorded separately from *Lepomis* raiders. Parental males appeared to treat all *Lepomis* raiders similarly. Catfish (*Ictalurus* spp.) and minnows (*Cyprinella* spp.) were also treated as raiders but bass

(*Micropterus salmoides*) and mosquito fish (*Gambusia affinis*) were ignored by parental males.

Hearing Sensitivity

Hearing sensitivity was determined using the auditory brainstem response (ABR) in collaboration with Dr. Hong Y. Yan at the University of Kentucky (Yan 1998; Yan 2001; Yan et al. 2000). Live fish (n = 5) were anaesthetized with gallamine triethioide (G-1137, Sigma Chemicals Co., St. Louis, Missouri, USA) placed in a small container of water in a soundproof chamber and electrodes were placed on the head. Pure tones were generated and played into the chamber using Tucker Davis Technologies electronic modules and software and the ABR was measured with increasing sound pressure level. During sound playback, ABR traces were based on average of 2000 sweeps per trial. Two ABR traces were generated, overlaid, and correlated to determine if the traces were repeatable. If the traces had an $r > 0.30$, the signal is determined to be above the hearing threshold (see Yan 2001 for more details).

Behavioral Analysis

Behavior of both sender and receiver were recorded during and immediately after calls. Both the general context and specific activity were recorded for the

parental male making the call. Specific behavior descriptions follow Miller 1963 (Table 18). The general context of sound production was recorded as either 'courtship', 'pursuit', or 'other'. Courtship calls were given during courtship activities and were easily recognized due to the presence of a ripe female and the distinctive courtship visual displays and movements of the male. Pursuit calls by the parental male were given during the pursuit of another fish, typically a raider. 'Other' calls were sounds produced while the male was sitting on the nest and were associated with fin flicks and jaw popping. These 'calls' are not discussed further since they are likely by-products of these movements, partially because there are rarely any other fish around the nest during this movement and they often occur after eating.

Specific behaviors during pursuit calls were categorized into one of three behaviors: 'chase', 'thrust', or 'rush'. A chase is a rapid movement toward another fish that is not only displaced by the territorial male but followed for some distance. A rush is a rapid movement toward another fish that is displaced by the sender but not followed. A thrust is a movement toward another fish, but without displacing it. These three behaviors were sometimes accompanied by lateral displays. There were also some pursuit calls given during courtship activities. Calls to females were made by a parental male while chasing a ripe female that he had either already courted or spawned with and will be included in the discussion of courtship calls.

Specific behaviors during courtship calls were more varied and consisted of several behaviors that could be displayed in rapid succession without a pause in calling: ‘in nest’, ‘surfacing’, ‘semi-surfacing’, ‘circle swimming’, ‘swimming around nest’, or ‘leading’. Lateral displays were occasionally given either in conjunction with or in between these behaviors. Unfortunately, it is difficult to determine the number of possible times the male could have called versus the number of the actual times, because it is difficult to determine the presence of a female and whether a male is not calling because he is not ‘interested’ (either due to presence of larvae or an ill-prepared nest) or because the female is not ripe.

Category	Behavior	Description
Maintenance	Feeding	Not observed
Maintenance	Sleeping	Not observed
Maintenance	Yawning	Usually after moving gravel or substrate around
Maintenance	Body Bend/Chafing	Infrequent; appears to be response to skin irritation
Maintenance	Fin Flickering *	Rapid up and down movement of dorsal, anal or pelvic fins
Maintenance	Fin Quivering	Side-to-side motion of dorsal, anal or caudal fins
Maintenance	Flapping pectorals	Not observed; pectorals rubbed against body
Maintenance	Jerking/Jerk Swimming *	Instantaneous bending of body, sometimes followed by short burst of swimming
Maintenance	Mouth snapping	Mouth opens and shuts rapidly and sporadically
Maintenance	Coughing	Often accompanied by spitting out nest debris
Agonistic	Thrust *	Move a short distance toward another fish; more often to neighbor males than raiders
Agonistic	Rush *	Move toward and displace another fish
Agonistic	Chase *	Move toward, displace and follow another fish
Agonistic	Swipe	Swims in arc toward another fish
Agonistic	Biting Movements	Directed toward intruder
Agonistic	Opercle spreads	Flaring of opercles and ear flaps; common to neighbor males, rare to females or raiders
Agonistic	Tail beating	Rare in the field - only when one parental male is trying to take over another parental male's nest
Agonistic	Attitude of inferiority	Females use while assessing and courting males
Agonistic	Mouth Fighting	Observed rarely among neighbor males

Table 18. Description of non-reproductive parental male behaviors. * indicates behavior is associated with sound production (not necessarily communication). # indicates behavior was added for this study and not present in Miller's (1963) original description.

Category	Behavior	Description
Nest Building	Sweeping/Digging	Vertical position using caudal fin to dig nest
Nest Building	Fanning	Move water over eggs using pectoral/caudal fins
Nest Building	Examine #	Visual inspection of the ground
Nest Building	Substrate Bite	Male uses to move gravel; females do frequently during courtship
Nest Building	Rim Circle	Patrol of nest by circling edge of nest, either due to raiders or females
Courtship	Circling/Swimming Around Nest #	Similar to rim circle but not clearly perimeter patrol
Courtship	Leading *#	Male leaves nest, circles around female and tries to lead her to his nest
Courtship	Surfacing *#	Distinctive courtship display, male at 45° accompanied by shaking
Courtship	Circle Swim *#	Very rapid swimming around nest and female
Courtship	Chase Female *#	Male chases courting/spawning female out of nest
Courtship	Tilting	Male and female tilting in unison to release gametes

Table 19. Description of parental male behaviors during reproduction, unless noted otherwise. * indicates the behavior is associated with sound production (not necessarily communication). # indicates that the behavior was added for this study and not present in Miller's (1963) original description.

Call Analysis

Calls were digitized from Hi-8 tape onto an IBM-PC computer using a Turtle Beach Tahiti™ sound card and signal analysis was performed in MATLAB (Version 5.3, Release 11, The Mathworks Inc, 1999) using damped sinusoid

discrete wavelet transforms (see Chapter 2 for details). Dominant frequency is the mode within a pulse with the highest energy, second frequency is the mode with the second highest energy. Mean frequency is the weighted average frequency of a pulse calculated by weighting each mode by its energy. Minimum frequency is the mode with the lowest frequency, while maximum frequency is the mode with the highest frequency. Pulse duration is the time difference between the first mode and last mode, or the duration of the longest mode. Rise time is the time difference between the first mode and the dominant frequency mode. Fall time is the time difference between the last mode and dominant frequency mode. Inter-pulse interval is the time difference between the last mode of one pulse and the first mode of the next pulse. Pulse rate (for calls with more than 1 pulse) was calculated by number of pulses/call duration. Call duration was calculated by subtracting the first mode of the first pulse from the last mode of the last pulse in a call. Means, medians and ranges are generated from raw data, while coefficients of variation (CV) and statistical analyses were calculated from transformed data. Frequency data were transformed using $\sqrt{x+\frac{3}{8}}$, while time data were transformed using $\sqrt{x}+\sqrt{x+1}$ in order to normalize the Poisson distributed data (following Zar 1999).

Descriptive and analytical statistics were conducted in Systat (Version 10,

SPSS, Inc., 2000). Nested MANOVA tests, with individuals nested within spawning success, was used to evaluate whether males that spawned had different calls than those that were not observed to spawn. Comparisons between contexts used paired t-tests on transformed data to examine differences in both means and standard deviations. Pearson correlations with Bonferroni corrections were used to assess how different parameters were related to each other and to behavioral and environmental parameters. Due to the large number of call parameters, exploratory statistics were used to understand the variation in calls between contexts. Principal components analysis (PCA) was used to determine which parameters contributed to the variation within each call context. Discriminant function analysis (DFA) was used to determine which parameters were useful for classifying pursuit and courtship calls.

RESULTS

Hearing Sensitivity

The audiogram in Figure 15 indicates that longear sunfish hearing sensitivity is greatest near 150 Hz, with good sensitivity between 100 and 200 Hz, moderate sensitivity between 200 - 400 Hz and poor sensitivity below 75 Hz and above 600 Hz. In other words, sounds at 75 and 600 HZ would have to be approximately 20 dB louder in order for a longear sunfish to hear them compared to

sounds at 150 Hz. This corresponds with the predominant energy in both courtship and pursuit calls which falls between 100 - 300 Hz. In addition, this matches the 'window' of best sound transmission in longear sunfish habitat between 75 and 200 Hz, with best transmission at 150 Hz (see Chapter 4 for more details).

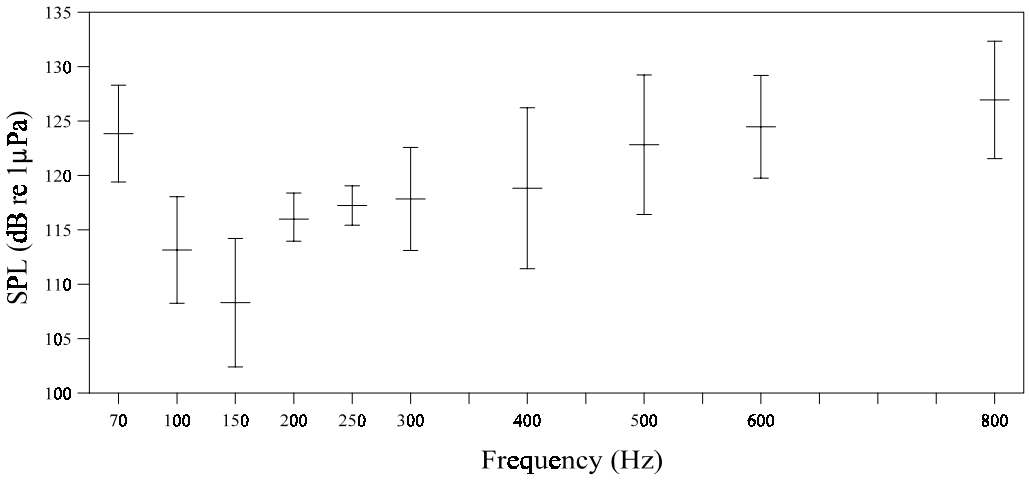

Figure 15. Audiogram based on auditory brainstem response. Sound pressure level (SPL) indicates sound intensity. Average threshold ± 1 standard deviation based on 5 fish. In collaboration with Dr. Hong Yan. Best sensitivity for all fish was 150 Hz.

Sender Behavior

Within a communication system, there needs to be at least one sender and one receiver. In longear sunfish, the typical sender is a parental male and the typical receiver is either a ripe female or a raider. The behavior of the sender, a parental male, was analyzed in two ways. First, behavior of 13 males was analyzed

during three 4-minute samples recorded in a single afternoon, for a total of 12 minutes per male. Four minute samples were reasonable estimates of the male's behavior, while reducing necessary video analysis. This analysis included all behavior, not just behavior associated with sound production. Second, the behavior associated with every call made by a male was determined, unless he was not visible on the video. Both analyses used the behavioral categories proposed by Miller (1963) for *Lepomis gibbosus* and *L. megalotis megalotis* (Table 18). However, 'examining', 'swimming around nest', and 'chasing females' were added - either due to the focus on sound production or because *L. m. aquilensis* used behaviors not used in the subspecies studied by Miller (1963). Many of the maintenance behaviors that seemed to involve skin irritation ('chafing', 'jerking', 'jerk swimming') appeared to be more frequent at the most urbanized sites (pers. obs.).

While pursuit calls were typically 1 - 2 pulses with an average of 1.4 pulses, courtship calls ranged from 1 - 50 pulses with an average of 4.2 pulses. There do not appear to be any trends with pulse number, so to simplify the results and discussion, all data are presented as individual pulses, not as data averaged for a call, unless stated otherwise (see Correlations in Chapter 4 for more details).

Courtship Calls

Courtship calls were produced by parental males in the presence of a ripe female either in or near his nest. It was rare that more than one ripe female was present in a colony at any given time. A female also never spawned without at least a few courtship calls. Courtship calls were associated with a variety of courtship behaviors (Table 20). Courtship calls were produced most frequently when the male was engaged in a surfacing display. The 'surfacing' display is the primary and distinctive visual display associated with courtship. The male approaches the surface at an angle while bending back and forth in light to reflect the colors on his body. Courtship calls were also given frequently when the male was hovering 'in the nest', either between surfacing displays or while a female hovered nearby. Calls were also often associated with the male 'swimming around the nest' or 'leading' the female into his nest. Males swam around the nest between surfacing displays and when a female was hovering near the nest or slowly approaching the nest. Males performed a leading display by approaching a female near his nest, and turning and attempting to lead her back to the nest. Females did not always follow. Males also frequently performed a very rapid 'circle swim' around the rim of the nest. Circle swims were infrequently associated with a call though they were frequently associated with a movement sound. Males also occasionally pursued a female out of the nest, typically after a period of spawning activity. The male usually did some egg tending and the female usually returned after 15 - 30 minutes

to resume spawning. Only one male that already had offspring called.

Fifty-two percent of all courtship behaviors (n = 5 males) were associated with calls. Eighty-two percent of surfacing displays were associated with calls (Behavior %, Table 20, Figure 16), and 59 percent of all courtship calls were produced during surfacing displays (Overall %, Table 20, Figure16). Fifty-five percent of the time in the nest during active courtship was associated with calls, while 21 percent of all courtship calls were produced while the male was in the nest. Twenty percent of the time spent swimming around the nest during active courtship was associated with calls, while only 8 percent of all courtship calls were produced while a male was swimming around the nest.

Courtship	Behavior %	Overall %	Dom Freq (Hz)	Pulse Duration (sec)
All Courtship	52 (n=53/101)		219 (0.22)	0.047 (0.06)
In Nest	55 (n=23/42)	21 (n=335)	220 (0.20)	0.043 (0.06)
Swim Around Nest	20 (n=3/15)	8 (n=130)	216 (0.19)	0.040 (0.06)
Surfacing	82 (n=18/22)	59 (n=927)	221 (0.21)	0.049 (0.06)
Circle Swim	75 (n=3/4)	2 (n=28)	183 (0.31)	0.057 (0.07)
Leading	75 (n=6/8)	8 (n=126)	203 (0.22)	0.047 (0.06)
Chase or Thrust	n/a	2 (n=25)	251 (0.31)	0.059 (0.07)

Table 20. Summary of parental male behavior during courtship calls. Behavior % is based on the detailed behavioral data set pooled across males and is the % of all instances of that behavior associated with a call. The three columns on the right are based on the courtship call data set. Overall % is based on the call data set used in all analyses and is the % of calls associated with a given behavior. The dominant frequency (Hz) and pulse length are means (CV in parentheses) for the appropriate context. Sample size indicates number of calls (from 5 males for Behavior % and 50 males for Overall %).

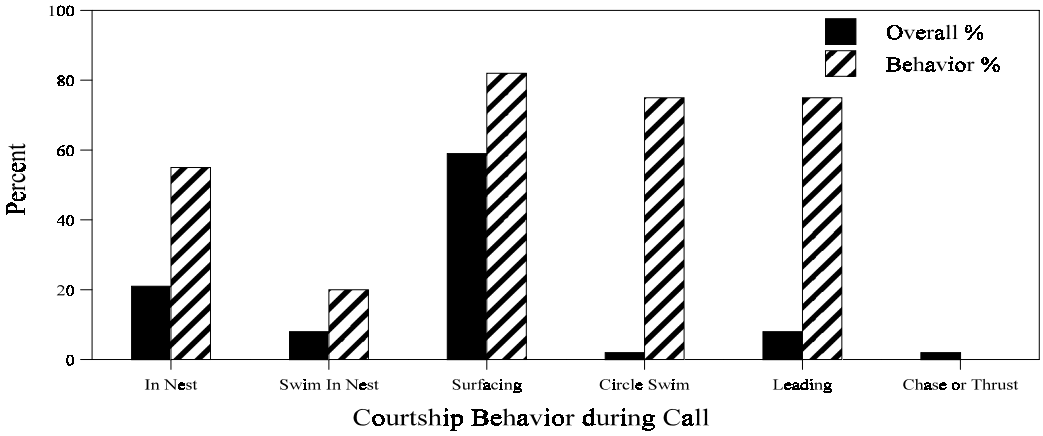

Figure 16. Bars in black are percentage of all courtship calls that occurred during this behavior (Overall % Table 20; i.e., 59% of all courtship calls were given when the parental male was surfacing). Bars with hatching are the percentage of behaviors in that context associated with a call (Behavior % Table 20; i.e., 82% of surfacing displays were associated with a call).

Courtship calls were given in a series of pulses with a mean of 4.2 pulses, a median of 3.0 pulses and a range from 1 - 50 pulses. The number of pulses appeared to depend on number of receptive and courting males within a colony and the size of the female (pers. obs.). Courtship calls sounded like a grunt, with a broad band, non-harmonic structure (Figure 17). For courtship calls across all males and all sites, the mean dominant frequency was 219 Hz and the mean pulse duration was 47 msec (see Table 21 for mean, median, range, and CV for all call parameters and Chapter 4 for discussion of variation among males and among sites).

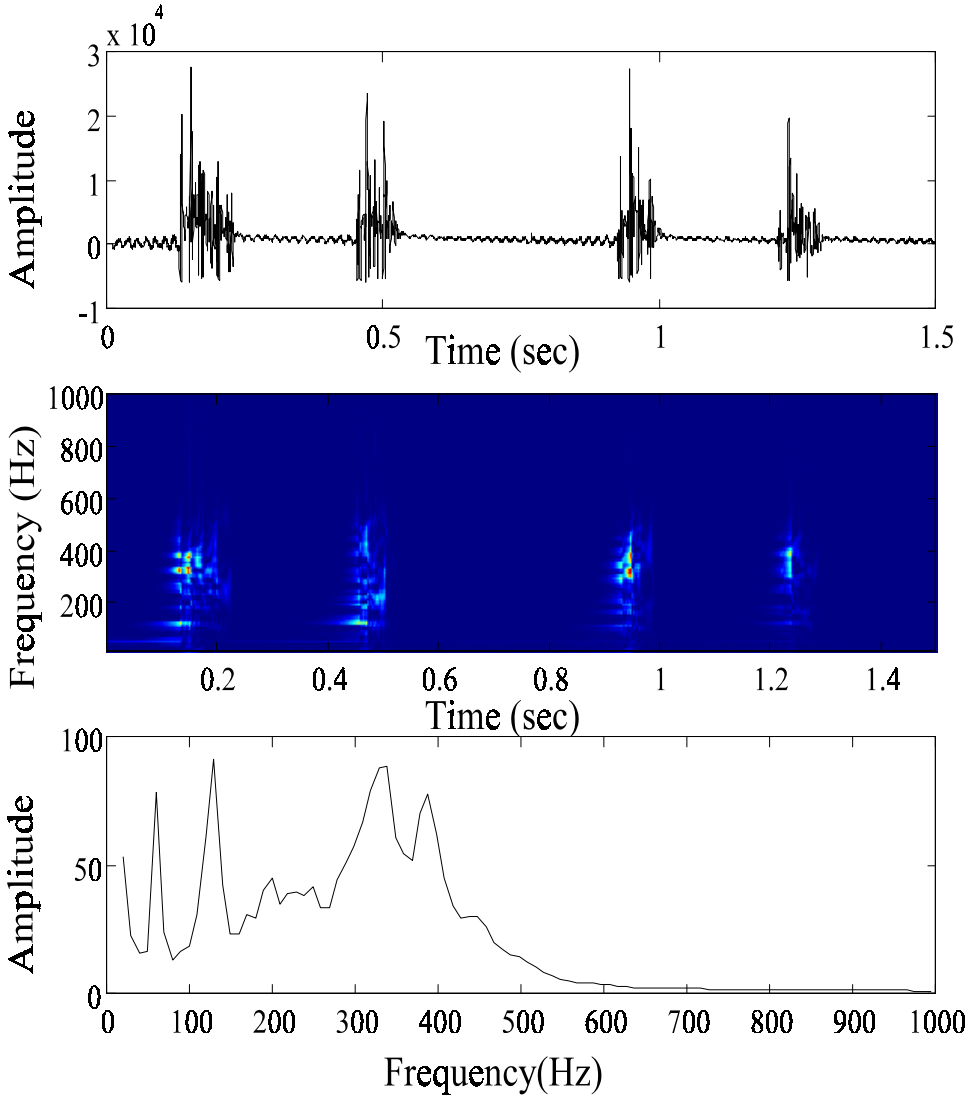

Figure 17. Courtship call from a parental male *Lepomis megalotis*. The waveform indicates four pulses. The wavelet derived spectrogram is based on a maximum threshold of 1000 Hz, 100 frequency bins, and wavelet damping rate of -0.15. The wavelet derived power spectrum is based on the sum of the information across time in the spectrogram.

Call Parameter	Mean	Median	Range	CV
Dominant Frequency (Hz)	219	201	30 - 742	0.22
Second Frequency (Hz)	242	223	15 - 699	0.24
Mean Frequency (Hz)	232	229	71 - 757	0.16
Minimum Frequency (Hz)	101	93	15 - 742	0.35
Maximum Frequency (Hz)	419	415	75 - 948	0.16
Pulse Duration (msec)	47	43	0 - 194	0.06
Rise Time (msec)	16	14	0 - 125	0.07
Fall Time (msec)	31	28	0 - 143	0.06
Inter-pulse Interval (msec)	422	344	1 - 2,691	0.15
Call Duration (msec)	1,563	929	2 - 23,122	1.35
Pulse rate (pulses/sec)	2.6	2.4	0.19 - 11.30	0.61
Number of Pulses	4.2	3	1 - 50	1.11

Table 21. Summary of call parameters for all courtship calls (n = 1786 calls, 50 males). See Methods for description of parameters. Mean, median and range were calculated from raw data, CV was calculated from transformed data.

To evaluate whether spawning success was related to call parameters, males that were observed spawning were compared to males that were not observed spawning. It is possible that a male spawned after or before the observation period and it simply was not recorded. There were significant differences between males that spawned and males that did not (nested MANOVA, $F = 3.973$, $p = 0.000$) for every call parameter (univariate ANOVA, all $p = 0.000$) when males were nested within spawning success. In addition, only males that were observed spawning produced calls with more than 18 pulses.

Pursuit Calls

Pursuit calls were given during a fairly restricted set of behaviors: chases, rushes, or thrusts. They were usually given after courtship had started or eggs had already been laid. Thirty-seven percent of all chases given by a male were accompanied by a call, while only 21 percent of all rushes were accompanied by a call, and only 3 percent of all thrusts were accompanied by a call (Behavior %, Table 22, Figure 18). Conversely, forty-nine percent of all pursuit calls were associated with a chase, 48 percent with a rush, and 3 percent with a thrust (Overall %, Table 22, Figure 18). In order to avoid analyzing sounds that resulted from bites or hits, I was conservative at designating chase calls, so the percentage of chase calls may be an underestimate.

Pursuit	Behavior %	Overall %	Dom Freq (Hz)	Pulse Duration
Pursuits with Calls	14 (n=124/889)		228 (0.39)	0.037 (0.09)
Calls with Chase	37 (n=58/158)	49 (n=530)	226 (0.37)	0.040 (0.09)
Calls with Rush	21 (n=59/275)	48 (n=523)	230 (0.41)	0.035 (0.08)
Calls with Thrust	3 (n=6/195)	3 (n=34)	251 (0.36)	0.027 (0.08)

Table 22. Summary of parental male behavior during pursuit calls. Behavior % is based on the detailed behavioral data set pooled across males and is the % of all instances of that behavior associated with a call. The three columns on the right are based on the pursuit call data set, except the rare contexts (see discussion above). Overall % is based on the call data set and is the % of calls associated with a given behavior. The dominant frequency and pulse length are means (CV in parentheses) for the appropriate category. Sample size indicates number of calls (from 13 males for Behavior % and 129 males for Overall %).

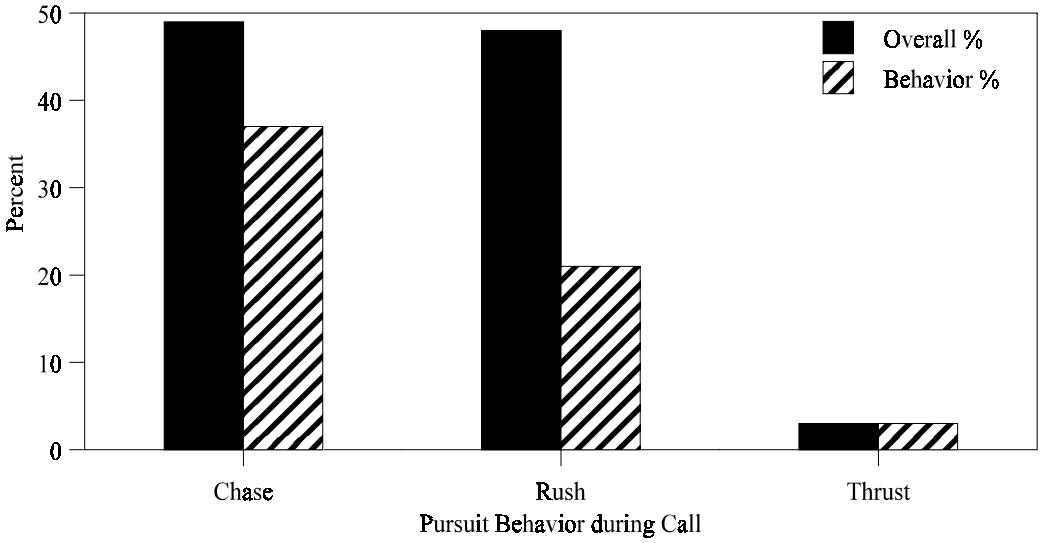

Figure 18. Bars in black are percentage of all pursuit calls that occurred during a given behavior (Overall % Table 22; i.e., 49% of all pursuit calls were given when the parental male was chasing). Bars with hatching are the percentage of behaviors in that context associated with a call (Behavior % Table 22; i.e., 37% of chases were associated with a call).

As reflected in the coefficients of variation for the dominant frequency and pulse lengths in Tables 21 and 23, pursuit calls were more variable than courtship calls. CVs for courtship calls ranged from 0.06 to 0.35, while CVs for pursuit calls ranged from 0.08 to 0.47. Pursuit calls varied from a broad band, non-harmonic grunt to a narrow band, non-harmonic pop (Figure 19). Mean dominant frequency was 227 Hz and mean pulse duration was 39 msec for pursuit calls (see Table 23 for mean, median, range, and CV for all call parameters).

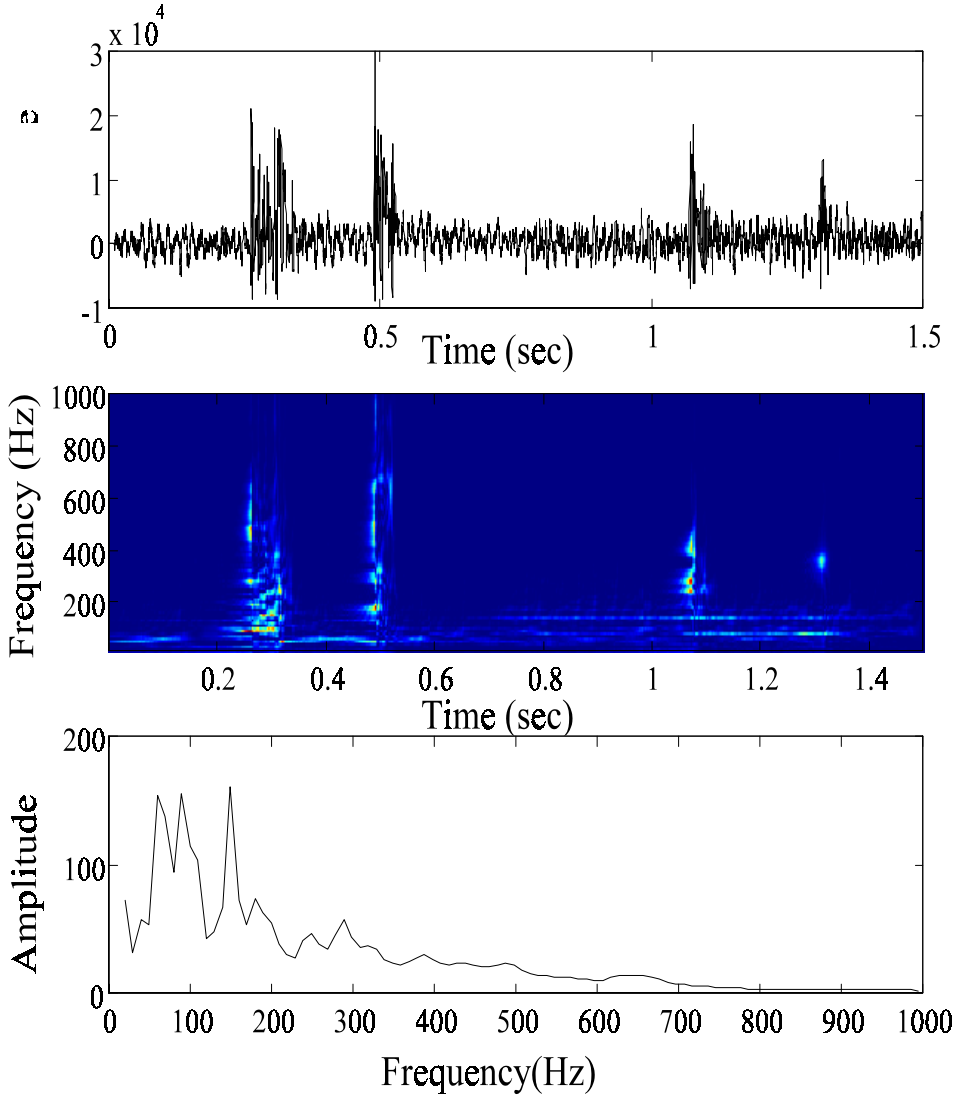

Figure 19. Two pursuit calls of two pulses each from a parental male *Lepomis megalotis*. The wavelet derived spectrogram is based on a maximum threshold of 1000 Hz, 100 frequency bins, and a wavelet damping rate of -0.15. The wavelet derived power spectrum is the sum across time from the spectrogram.

Call Parameter	Mean	Median	Range	CV
Dominant Frequency (Hz)	227	179	14 - 1043	0.39
Second Frequency (Hz)	248	209	15 - 1044	0.38
Mean Frequency (Hz)	239	219	24 - 815	0.30
Minimum Frequency (Hz)	90	65	14 - 674	0.45
Maximum Frequency (Hz)	508	490	60 - 1279	0.45
Pulse Duration (msec)	39	27	0 - 249	0.09
Rise Time (msec)	15	6	0 - 204	0.08
Fall Time (msec)	24	15	0 - 227	0.08
Inter-pulse Interval (msec)	269	159	5 - 2,042	0.24
Call Duration (msec)	156	54	1 - 3,320	1.98
Pulse Rate (pulses/sec)	7.25	4.99	0.49 - 64.52	1.79
Number of Pulses	1.4	1	1 - 6	0.49

Table 23. Summary of call parameters for all pursuit calls (n = 1325 calls, 129 males). See text for description of parameters. Mean, median and range were calculated from raw data, while CV was calculated from transformed data.

Receiver Behavior

To assess call function, videotapes were analyzed to determine receivers' reactions to calls from different behavioral contexts. Notably, no calls were ever used with other territorial males. Altercations between neighbors were completely silent. Interestingly, opercle spreads, a distinctive visual display with flared opercles, were observed exclusively in interactions with neighbors.

Courtship Calls

Based on 1386 interactions with 39 parental males, courtship calls only

occurred when a female was in the vicinity of the nest (see Table 24 and Figure 20 for results). In 4 cases, no ripe female was visible on the video, although one had been observed in the colony the same day. Female responses ranged from remaining near the nest, entering the nest, staying in the nest for varying lengths of time, to actively circling with the male.

Courtship Calls	Near Nest	Enters Nest	In Nest 1-10 sec	In Nest >10 sec	Leaving Nest	Circle W/ Male
Leading	8 (104)	0.8 (12)	0	0	0.2 (4)	0
In Nest	5 (71)	8 (107)	4 (52)	1 (18)	0.6 (8)	0.1 (1)
Swimming	1 (13)	3 (36)	3 (45)	1 (16)	0	0.5 (7)
Surfacing	11 (152)	17 (241)	22 (302)	9 (124)	0.3 (4)	3 (41)
Pursuit	0.6 (8)	0	0	0	1 (14)	0
Total	25 (348)	29 (396)	29 (399)	11 (158)	2 (30)	4 (49)

Table 24. Summary of female response to courtship calls. Each cell indicates % females' reactions in response to calls in the left column. Number of encounters in parentheses.

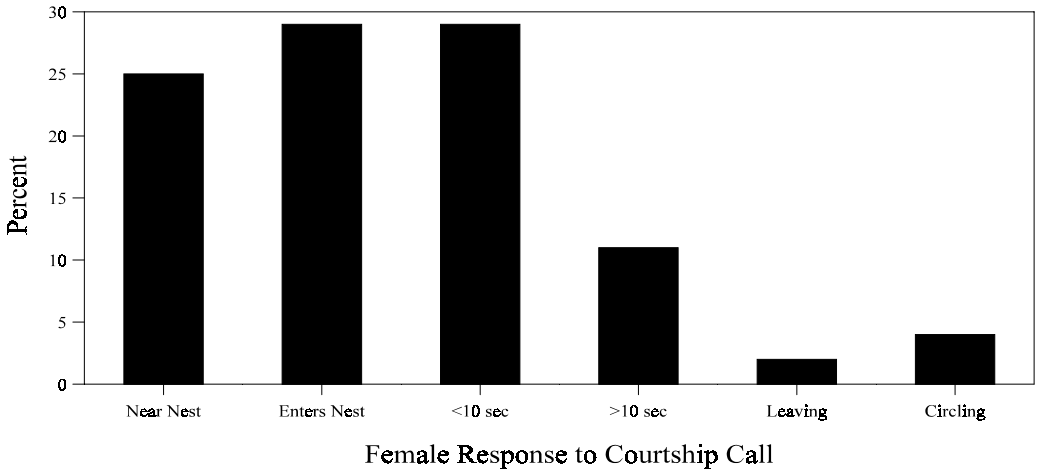

Figure 20. Response of ripe females to courtship calls from parental males.

Pursuit Calls

Based on 374 interactions with 58 parental males, it is clear that receivers respond to pursuit calls by moving away from the nest in one form or another (see Table 25 and Figure 21 for results). The receiver always responded or reacted to pursuit calls. Fifty-seven percent of calls resulted in the receiver swimming away and not returning to the nest, while only twenty-five percent resulted in the receiver swimming away and returning. Individuals that did return often swam away eventually, after repeated pursuits from the parental male. Most, if not all, of the receivers that changed course (11%) were fish just swimming by that were deflected from passing over the nest by the male.

Pursuit Calls	Backed Off	Changed Course	Swam Away, Returned	Swam Away, No Return	Hid
Chase	0.5 (2)	4 (13)	7 (26)	37 (137)	0
Rush	5 (18)	8 (29)	18 (66)	20 (73)	0.3 (1)
Thrust	1 (5)	0.3 (1)	0.3 (1)	0.5 (2)	0
Totals	7 (25)	11 (43)	25 (93)	57 (212)	0.3 (1)

Table 25. Summary of receiver response to pursuit calls. Each cell indicates the percentage of receivers reactions in each category in response to the males' behavior associated with a call in the left column. The number in parenthesis is the sample size.

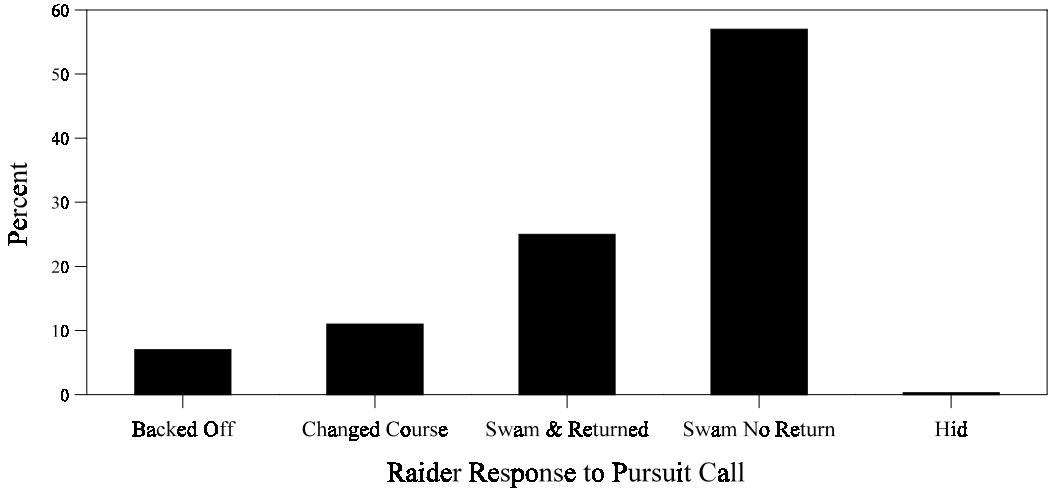

Figure 21. Response of raiders to pursuit calls from parental males.

Structural Differences Among Contexts

Differences between courtship and pursuit calls were examined using a subset of the data that included only males (n = 10) for which there were at least 5 calls from each context. Both differences between means and standard deviations were examined using paired t-tests on transformed data (Figures 22 and 23). Mean frequency ($p = 0.036$) and rise time ($p = 0.028$) showed significant differences in means between contexts. Standard deviations of dominant frequency, second frequency, mean frequency, maximum frequency and pulse rate showed significant differences between contexts ($0.002 < p < 0.014$). In other words, mean frequency exhibits differences in both value and variation between contexts, rise time exhibits differences in value only while pulse rate, dominant, second, and maximum

frequency exhibit differences in variation only.

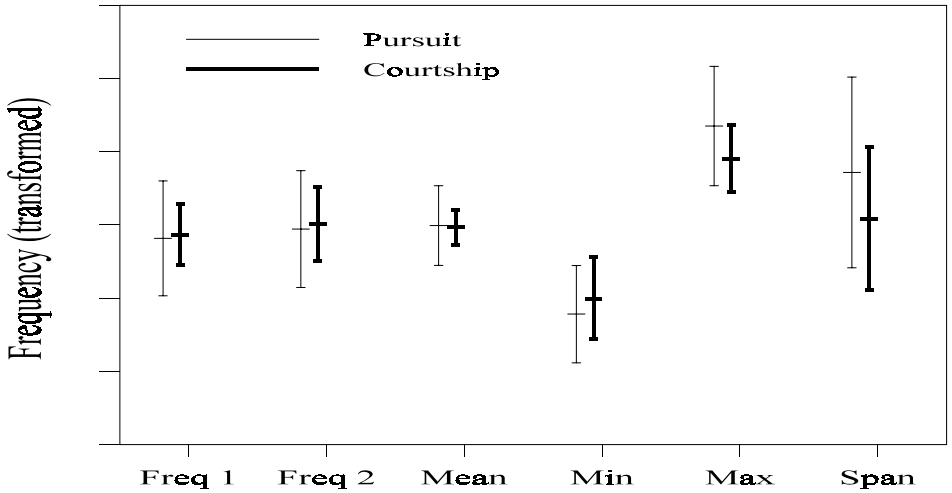

Figure 22. Plots of average ± s.d. of transformed data (See Methods for transformation) for spectral call parameters of the data subset used for context comparisons. Pursuit calls are light lines on left, courtship calls are heavy lines on right.

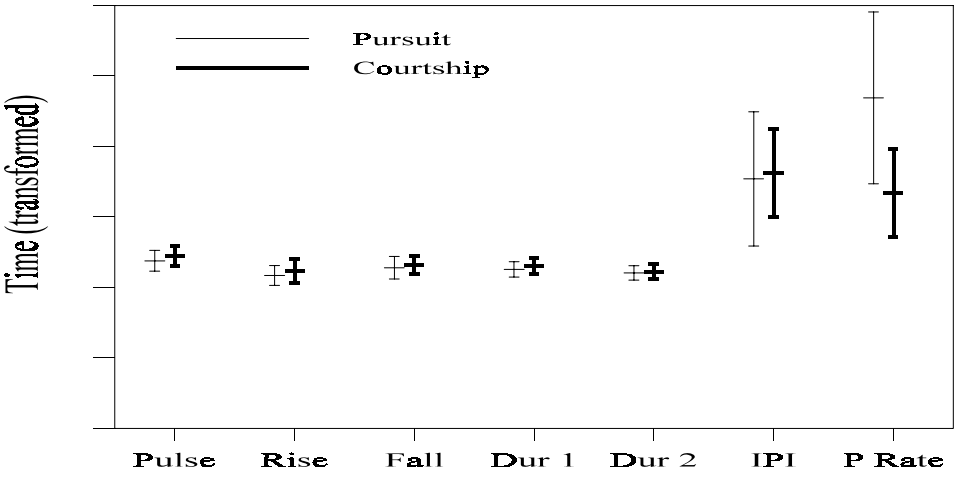

Figure 23. Plots of average ± s.d. of transformed data (See Methods for transformation) for temporal call parameters for the data subset used for context comparisons. Pursuit calls are light lines on left, courtship calls are heavy lines on right.

Factor loadings from principal components analysis (PCA) (Table 26) indicate which call parameters contribute to call variation and explore how context relates to overall call variation. Mean frequency, dominant frequency, pulse duration and duration 1 were important for explaining variation. Pulse rate, call duration and rise time were relatively unimportant. The first factor explained 32% of the variation, while the second factor explained 17%. Figure 24 shows a plot of the scores for the first two factors coded by context. The same factor loadings coded by site are in Figures 33 and 34 in Chapter 5.

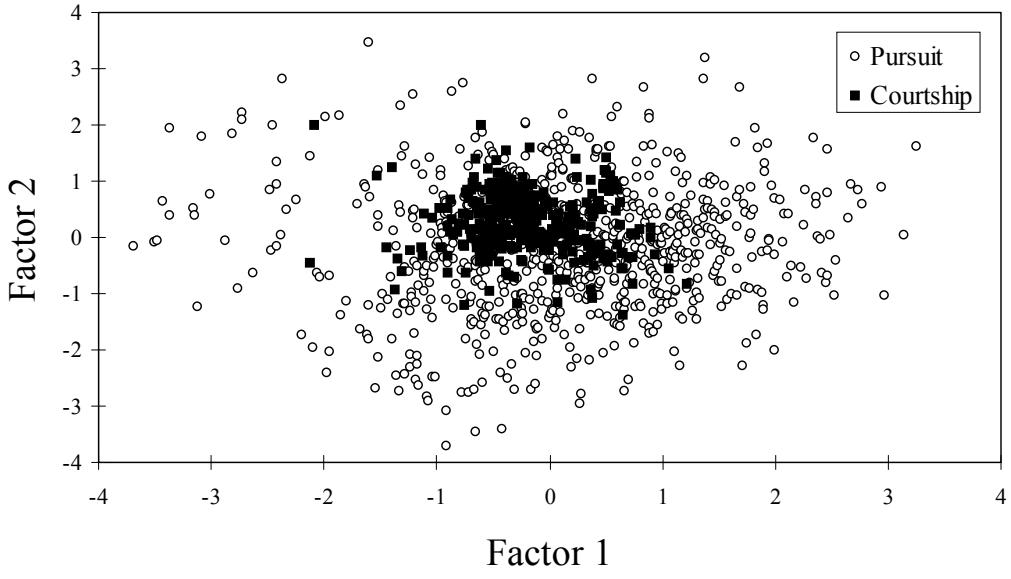

Figure 24. Plot of factor loadings for first two factors from principal components analysis (PCA) using call averages and coded for context.

A backwards step-wise discriminant function analysis (DFA) was performed to evaluate which parameters were useful in categorizing calls to the correct context. Factor loadings for the first factor are given in Table 26. This function classified 87% of calls correctly to context. Dominant frequency, frequency span, and pulse rate were removed during the step-wise DFA and therefore were not useful for correct classification. Call duration and pulse duration were the most important parameters for classification.

Call Parameter	**PCA**	**DFA**
Dominant Frequency	0.718	--
Second Frequency	0.609	0.121
Mean Frequency	0.818	0.393
Minimum Frequency	0.475	-0.117
Maximum Frequency	0.599	-0.470
Frequency Span	0.428	--
Pulse Duration	-0.688	-0.532
Rise Time	-0.353	0.511
Fall Time	-0.604	0.497
Duration 1	-0.721	0.273
Duration 2	-0.569	0.276
Call Duration	-0.189	0.830
Pulse Rate	0.017	--
	% Variance = 32	% Correct = 87

Table 26. Factor loadings for the first factor for principal component (PCA) and discriminant function analyses (DFA) for all calls. – means the parameter was removed during stepwise DFA.

Correlations Among Call Parameters

The acoustic properties of a signal can be studied by using correlations to understand how different call parameters contribute to call structure. The relationship of acoustic properties to behavioral and ecological parameters can also be studied using correlations. 'Trivial' correlations, that is where one parameter is used to generate another parameter, are indicated in Table 27 with a slash through the box. It is interesting that dominant frequency and second frequency were not correlated. In addition, rise time and fall time were not correlated, even though they additively constitute pulse duration. Duration 1 was correlated with dominant and mean frequency in pursuit calls, but it was correlated only with fall time in courtship calls.

Pulse rate and inter-pulse interval were correlated only with each other (Pearson $r = 0.63$ courtship, 0.66 pursuit), but exhibited no $r > 0.26$ with any other parameters. For both courtship and pursuit calls, dominant frequency and second frequency were correlated with mean frequency, but not with each other (Table 27). Mean frequency was also correlated with maximum frequency for both contexts, but only with minimum frequency in pursuit calls. Frequency span was correlated with maximum frequency for both courtship and pursuit calls, but only with minimum frequency in courtship calls. Pulse duration was correlated with rise time, fall time and duration 1 for both contexts, and fall time and duration 1 were

correlated. Duration 2 was not strongly correlated with any other parameter. The only frequency parameters that correlate with temporal parameters were dominant frequency and mean frequency with duration 1, but only for pursuit calls.

	Freq1	Freq2	Mean	Min Freq	Max Freq	Freq Span	P Dur	Rise	Fall	Dur1	Dur2
Freq1		*0.24*	***0.77***	*0.17*	*0.26*	*0.14*	*0.10*	*0.00*	*0.10*	*0.39*	*0.00*
Freq2	0.40		***0.59***	*0.22*	*0.37*	*0.20*	*0.10*	*0.00*	*0.00*	*0.14*	*0.33*
Mean	**0.86**	**0.66**		*0.24*	***0.57***	*0.35*	*0.00*	*0.00*	*0.10*	*0.32*	*0.14*
Min F	0.47	0.42	**0.52**		*0.10*	***0.51***	*0.41*	*0.20*	*0.35*	*0.26*	*0.33*
MaxF	0.41	0.46	**0.64**	0.10		***0.87***	*0.00*	*0.00*	*0.14*	*0.00*	*0.00*
FSpan	0.17	0.28	0.35	0.26	**0.88**		*0.33*	*0.14*	*0.30*	*0.17*	*0.20*
P Dur	0.33	0.22	0.32	0.37	0.10	0.17		***0.54***	***0.71***	***0.52***	*0.41*
Rise	0.17	0.10	0.14	0.20	0.10	0.10	**0.69**		*0.10*	*0.00*	*0.14*
Fall	0.24	0.20	0.22	0.36	0.00	0.14	**0.77**	0.20		***0.54***	*0.37*
Dur1	**0.57**	0.24	**0.53**	0.33	0.20	0.00	**0.60**	0.28	0.48		*0.40*
Dur2	0.24	0.46	0.30	0.35	0.00	0.10	0.49	0.32	0.42	0.40	

Table 27. Pearson r correlations among call parameters. Two triangular correlation matrices are presented. Correlations for pursuit calls are in bottom left. Correlations for courtship calls are in top right in *italics*. Though all r > 0.30 were significant at the p = 0.05 level with Bonferroni corrections, only r > 0.50 are in **bold**. Boxes with a slash indicate 'trivial' correlations due to mathematical dependence.

Correlations with Behavior and Environment

Call parameters can be correlated with other parameters that are directly under selection, such as body size, or environmental parameters, such as background noise. This may cause some of the variation that is discussed in Chapter 5. Within pursuit calls, some p-values were highly significant, however, correlations were weak with none > 0.22 (Table 28). Body weight was correlated with dominant frequency and mean frequency. Time of day was correlated very weakly with minimum frequency. Stream temperature was correlated weakly with minimum frequency, rise time, and pulse duration. Pulse number (pulse was 1st, 2nd, etc) was correlated with many parameters, however, this was likely due to there being only 10 pursuit calls (out of 956 pursuit calls overall) with four, five, or six pulses (from 8 males, 5 from Walnut Creek). While the correlations were significant, I am reluctant to suggest they were biologically meaningful, with so few calls with more than three pulses and very low correlations. When calls with > 3 pulses were excluded, there were no correlations between pulse number and any call parameter. Background noise, nest status (empty, eggs, hatchlings or wrigglers), and male behavior during calling (thrust, rush, or chase) were not correlated with any call parameters.

	Weight	Fork Length	Nest Status	Specific Behavior	Bgd. Noise	Time	Temp	Pulse No.
Freq1	0.17	0.14						0.10
Freq2	0.10	0.10	0.10					0.10
Mean	0.20	0.17						0.14
Min	0.10	0.10				0.10	0.14	0.20
Max	0.14	0.10						
Span	0.10	0.10					0.10	0.10
P Dur	0.10	0.14					0.14	0.17
Rise	0.10	0.14			0.10		0.14	0.10
Fall	0.10	0.10					0.10	0.17
Dur1								0.17
Dur2	0.10	0.10					0.10	0.10
IPI	0.10	0.10				0.14	0.10	0.10
Call	0.12	0.13		0.20				
PRate						0.10	0.10	

Table 28. Pearson correlations among pursuit calls between pulses and environment and behavioral parameters. Empty cells indicate $r < 0.10$ with no $r > 0.30$ or $p < 0.05$.

Within courtship calls, there were significant correlations with a few $r > 0.30$ (Table 29). Body weight was correlated weakly with minimum frequency, pulse duration, and duration 2, but strongly with dominant frequency and frequency span. Fork length was correlated with minimum frequency, dominant frequency, and frequency span. Time of day was correlated with pulse duration and fall time. Approximate stream temperature was correlated with all parameters except dominant, second and mean frequencies. Background noise was correlated with

maximum frequency, frequency span, and rise time. Nest status was correlated with pulse duration, minimum frequency and pulse rate. Male behavior during calling (in nest, surfacing, swimming, pursuit) was correlated with mean frequency, inter-pulse interval, and pulse rate. Like pursuit calls, pulse number showed a few weak correlations that were likely generated by the 9 calls (out of 422) with many pulses (18 - 50 pulses/call). When calls with > 18 pulses were excluded the only remaining significant correlation was pulse duration ($r = 0.10$, $p = 0.04$).

	Weight	**Fork Length**	**Nest Status**	**Specific Behavior**	**Bgd. Noise**	**Time**	**Temp**	**Pulse No.**
Freq1	***0.35***	***0.35***		0.10				
Mean	0.10	0.10		0.10	0.10			0.10
Min	*0.17*	*0.17*	0.10				0.36	
Max	**0.37**	**0.37**			0.10	0.10	0.10	
Span	*0.30*	*0.33*			0.10		0.20	
P Dur	0.17	0.14	0.28		0.10	0.10	0.44	0.10
Rise	0.10	0.10	0.10		0.10		0.24	0.10
Fall	0.14	0.10				0.10	0.32	
Dur1		0.10	0.10				0.22	
Dur2	0.17	0.17				0.10	0.17	
IPI	0.10	0.10	0.10	0.14			0.26	
Call				0.21			0.10	
PRate	0.10			0.24		0.16	0.19	

Table 29. Pearson r correlations among courtship calls between pulses and behavioral and environmental parameters . $r < 0.10$ are empty cells. $r > 0.30$ are indicated in **bold**, comparisons with $p < 0.05$ are indicated in *italics*. Note high r does not indicate high significance and vice versa.

DISCUSSION

Previous work on acoustic signals in sunfish (Centrarchidae: Perciformes) described sound production during courtship by parental males (Gerald 1970, 1971; Ballantyne and Colgan 1978a,b,c). Gerald (1970, 1971) reported sound production from six *Lepomis* species from around Austin, Texas. Due to limitations of signal analysis, more detailed information on call structure was not available. Gerald's study (1970) was largely descriptive, based only on courtship calls and streamside observations with only one population per species. The present study differs by examining multiple populations within one species and by examining both courtship and pursuit calls. Recognition of pursuit calls and detailed behavioral analysis of both senders and receivers was facilitated in the present study by synchronization of video and audio.

Hearing sensitivity of longear sunfish is similar to that of bluegill sunfish (*Lepomis macrochirus*) (Yan et al. 1997). Both show best hearing sensitivity around 150 Hz and are insensitive to sounds above 800 Hz, which is consistent with sound production in these species with calls having high energy between 100 and 350 Hz. Centrarchid fishes are considered hearing generalists and possess no known adaptations to improve hearing (Popper & Fay 1993). As bluegill and longear sunfish often live and breed in the same habitat and have similar morphology and physiology (Rabeni 1990; Vadas Jr. & Orth 2000), it is not

surprising that the audiograms for the two species are similar.

Nesting males with offspring typically directed pursuit calls primarily toward raiders during rushes and chases. Recipients of pursuit calls typically responded by leaving the nest area, at least temporarily but frequently permanently. Nesting males with empty nests typically directed courtship calls exclusively toward ripe females during active courtship. Females typically responded by remaining in, near or approaching the nest. There are a variety of differences between courtship and pursuit calls. Courtship calls exhibit less variation on average in spectral parameters and pulse rate than pursuit calls, while mean frequency is lower and rise time is longer on average than pursuit calls. This is similar to the pattern seen in release and advertisement calls in frogs. Release calls typically vary substantially within and among individuals, but advertisement calls show less variation in most call parameters (Weber 1976). See Chapter 5 for further discussion of differences in variation between courtship and pursuit calls.

Based on correlations between sender and receiver behavior during sound production, possible functions for courtship and pursuit calls can be suggested. Given that courtship calls were only given when a ripe female was present, the calls were likely used by the female in mate selection or to stimulate female physiological readiness to mate. Females appeared to visit several males in a colony and to chose the male that displayed most vigorously (both visually and

acoustically, pers. obs.). There may be a substantial amount of behavioral feedback between male and female that elicits more calling behavior after the initial encounter. The courtship call is likely an important signal for the female in mate choice. Although it is possible that the call indicates body size, correlations between call parameters and body size are weak at best, and it is more likely to indicate vigor and/or interest. A male varied the intensity of his courtship calls over the course of a breeding cycle. When first establishing a nest, a male would produce a courtship call but usually only a few pulses and only to females that came into the nest. Once the nest was well-excavated and cleaned, a male would call vigorously and repeatedly to any ripe female in a colony. After a male had spawned and was caring for young, he never produced any courtship calls. Given that the difference a male producing courtship calls and not producing them was sometimes less than 24 hours, it seems likely that any information in courtship calls is related more to physiology than body size.

In contrast, the recipient of pursuit calls was typically a raider (although on occasion they were directed toward a female or sneaker male), who usually fled the nest once pursued. Persistent raiders may have required several pursuits, but ultimately they fled as well. The only occasions when pursuit calls were not effective were when the nest was overwhelmed by several dozen raiders at once. Usually, however, the male eventually succeeded at chasing off raiders, though it

took many minutes. This suggests a function in defensive behavior, in particular reinforcing the other behavioral and visual cues given during this type of encounter. Parental males usually started warning a raider by tracking its movement around the nest, then moved onto thrusts, then rushes and, if the raider persisted, finally to chases. If the parental male had to repeatedly chase the raider, the chases typically increased in length each time. As soon as a raider turned to flee and lost eye contact, visual signals no longer provided information while acoustic signals could still be perceived. Therefore it is not surprising that few thrusts were associated with calls, since raiders were more likely to back off than flee in response to a thrust and were not as likely to lose eye contact.

Reproductive behavior of *L. m. aquilensis* differs from at least three other subspecies (*L. m. megalotis*, *L. m. peltastes*, and *L. m. breviceps*) (Dupuis & Keenleyside 1988; Keenleyside 1972; Witt Jr. & Marzolf 1954). Interestingly, central Texas bluegill (*L. macrochirus*) differ from other populations of bluegill in the same way (Thompson 1998). In both species, central Texas populations lack breeding synchrony, except after a period of either flooding or drought, and there are very few female mimics probably because spawning males do not tolerate more than one 'female' in the nest at a time and typically cease all spawning activity until only one 'female' remains in the nest (pers. obs.). As a result, the success of alternate male mating strategies in these populations is reduced, which may affect

how pursuit calls are used. It is possible that pursuit calls in northern populations are used more frequently toward sneaker males and female mimics during spawning than they are in central Texas. This may result in different selection pressures on signal structure and use.

An interesting observation is that largemouth bass (*Micropterus salmoides*) were typically ignored by parental males. Bass were never observed to eat eggs or attack parental males. They were observed to chase females and raiders. This is in contrast to previous suggestions that colony formation is an anti-predator mechanism specifically against bass (Gross & MacMillan 1981). Indeed, the presence of bass seemed to reduce the number of raiders present around a colony (pers. obs.). Parental males were extremely aggressive towards catfish (*Ictalurus* spp.) and minnows (*Cyprinella* spp.), both of which foraged on the substrate and were observed to remove considerable numbers of young. The minnows particularly would forage through a colony as large groups and systematically raid each nest. If colonies are formed as an anti-predator device, it is more likely as a mechanism to 'swamp out' the raiding *Cyprinella* schools.

Courtship calls in longear sunfish, and many other fishes, seem to play a similar role as advertisement calls in frogs. Pursuit calls in longear sunfish seem to play a role similar to that of distress calls in frogs. The aggressive calls in frogs and in birds do not seem to have a parallel in longear sunfish. There were no acoustic

signals exchanged between neighboring territorial males. Communication was limited to visual displays, particularly opercle flares, and physical contests.

Sound production is common, if not ubiquitous, among territorial freshwater species, but less common in non-territorial species. Freshwater fishes appear to use acoustic signals in a similar manner as coral reef fishes, but slightly differently than estuarine fishes. Territorial coral reef and freshwater fishes use acoustic signals predominantly for short distance communication and occasionally in neighbor male encounters (e.g. Johnson 2000; Lobel & Mann 1995; Lugli et al. 1996; Myrberg et al. 1986; Salmon 1967; Stout 1975). Territorial estuarine fishes seem to use acoustic signals for both long and short range communication and they are used among neighbor males (Bass 1990; Brantley & Bass 1994; Fine 1978).

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Chapter 4
Acoustic Signal Propagation and Ambient Noise in Shallow Streams

Ambient noise and acoustic signal propagation were measured in a series of shallow (< 40 cm) freshwater streams in central Texas. Ambient noise levels from isolated creeks in nature preserves ranged from approximately 66 - 71 dB re 1 μPa at 100 Hz to 50 - 53 dB at 1000 Hz (n = 4 sites). Ambient noise from urban streams was approximately 83 dB at 100 Hz and 56 dB at 1000 Hz (n = 2 sites). I broadcast a series of pure tones from 50 to 1000 Hz and longear sunfish call exemplars were broadcast at five sites to assess signal propagation. In general, 75 - 200 Hz attenuated least across all streams indicating a 'window' for signal propagation in these shallow streams. The least transmission loss at all sites was at 150 Hz. Degradation above 200 Hz was similar among sites with approximately -18 dB for 50 cm, -27 dB for 100 cm, and -29 dB for 200 cm. Transects within a stream, as well as among streams, show some similarity but with no pattern. Signal transmission was surprisingly uniform across sites given the diversity of substrate types, water depths and current velocities. The majority of ambient noise impinges only slightly on, and the transmission window overlaps substantially with, the frequency range of stream fish calls. Based on dominant frequencies reported for the different taxa, fishes appear to take advantage of low frequency transmission

windows generated in the near field while insects appear to use high frequency windows generated in the far field.

INTRODUCTION

Many animals use acoustic signals to communicate at various stages of their life cycle and in many different contexts (Dusenbery 1992; Hauser 1996; Vehrencamp & Bradbury 1998). Signals are transmitted through different media, such as air, substrate, and water. The transmission of acoustic signals in air is reasonably well-understood and well-studied by physicists, biologists and engineers (e.g. Crocker 1998; Vehrencamp & Bradbury 1998; Gish & Morton 1981; Dabelsteen et al. 1993; Kime et al. 2000; Wiley & Richards 1978; Sutherland & Daigle 1998). Ambient noise windows have been described for ground level forest habitat and birds calling in that habitat tend to match spectral properties to the noise window (Morton 1975; Ryan & Brenowitz 1985). Transmission windows have been found in terrestrial systems (Penna & Solís 1998), but they are not as pronounced as in aquatic systems (see below and Richardson et al. 1995; Urick 1983; Horch & Salmon 1973; Aiken 1982). Many studies have reported that acoustic signals produced by birds, which use songs largely for long distance communication, are strongly influenced by the transmission properties of the environment (Brenowitz 1982; Gish & Morton 1981; Sorjonen 1986). This trend is

less pronounced or undetectable in acoustic signals in frogs (Kime et al. 2000; Penna & Solís 1998).

The majority of studies on sound transmission in air have focused on transmission in the far field, largely because the near field is very small in air (Vehrencamp & Bradbury 1998). The majority of studies on sound transmission in water have been conducted in the ocean over large distances and therefore also focus on the far field. The near field is the area over which molecular displacement occurs in addition to the pressure wave from the sound. The near field is not a rigid boundary but slowly tapers off. The near field in general, however, is much larger in water than air, such that for 150 Hz the near field is 1.6 m in water versus 0.4 m in air. Signals of fishes communicating over short distances are subject to more complicated phenomena than those signals traveling greater distances (Hawkins 1986; Urick 1983).

Transmission through water over long distances is well understood for deep open ocean systems (Brekhovskikh & Lysanov 1991; Kuperman 1998; Richardson et al. 1995; Urick 1983; Weston 1992). However, transmission of acoustic signals in fresh waters, especially in streams, rivers, and small ponds is poorly documented, difficult to model and presumed to be highly site-specific (Crawford et al. 1997; Richardson et al. 1995; Zakarauskas 1986). The development of theory on shallow water signal propagation is limited to the continental shelf (e.g. Zakarauskas 1986),

which is many orders of magnitude deeper than a typical stream. Theoretically, a signal in an acoustically ideal stream will exhibit cylindrical spreading (best represented via normal mode theory) instead of spherical spreading, as in the ocean or in most terrestrial habitats, due to the nearness of surface and substrate (Richardson et al. 1995). In an ideal environment, a transmission loss of -6 dB per doubling of distance is expected near the source (near field). After lower frequencies have been attenuated, a transmission loss of -3 dB per doubling of distance is expected at a distance from the source (far field) (Brekhovskikh & Lysanov 1991; Crocker 1998; Richardson et al. 1995; Urick 1983). Distance from the source where this transition occurs depends on several factors, particularly water depth. Factors influencing signal propagation in shallow water include type of substrate, temperature gradients, depth, and flow patterns (Crawford et al. 1997; Rogers & Cox 1988). Models for understanding ambient noise in shallow marine waters indicate that there is not likely to be homogeneity within a site, and that variation in substrate properties has substantial effects on signal propagation and ambient noise spectra (Richardson et al. 1995; Zakarauskas 1986). The frequencies transmitting best should be determined in part by the depth from the reflective surface to the rigid layer of the substrate, which may be below any overlaying mud or gravel.

There are only a few published studies on acoustic signal propagation in

water less than 2 m deep (Aiken 1982; Banner 1971; Crawford et al. 1997; Fine & Lenhardt 1983; Forrest et al. 1993; Horch & Salmon 1973). Banner (1971) reported on signal propagation of white noise and mechanical sounds in a 20 to 60 cm deep bay over a sandy mud bottom. Using both pressure and velocity hydrophones, Banner (1971) found that there was approximately 8 - 13 dB attenuation per distance doubling for continuous signals, while attenuation of pulsed signals was closer to 5 dB per distance doubling. Both pressure and velocity attenuated at similar rates in the horizontal plane, but velocity attenuated less in the vertical plane. Banner (1971) used very few frequencies (20, 40, 80, 160, 320, and 640 Hz), so there may not have been enough resolution to detect windows or portions of the spectrum that have better signal propagation properties than other parts of the spectrum (see Figure 29 for an example). Horch and Salmon (1973) reported such a window in their study of attenuation of squirrelfish (*Myripristis* spp.) grunts in wading pools at 0.5m and near a pier at 1.5m (with a water depth of 5m). They focused on 50 - 1000 Hz and attenuation was not quantified, but based on their graphs, there was approximately 5-10 dB loss per distance doubling, with 100 - 500 Hz showing less attenuation than other frequencies. Aiken (1982) reported on signal propagation of pure tones from 2500 - 7500 Hz at 21 cm depth over a gravel bottom. Of all frequencies tested, 5500 Hz and 6000 Hz attenuated least, which formed a window that matched the dominant frequencies of typical

aquatic insect calls. Fine and Lenhardt (1983) reported on signal propagation of pure tones and white noise from 30 - 4000 Hz in an estuary at 1m depth, where they found that 500 - 2000 Hz signals exhibited the least transmission loss. Forrest et al. (1993) reported on signal propagation using a sinusoidal sweep from 100 - 20,000 Hz in a shallow, muddy pond at 13 and 45 cm depth. Frequencies below 500 Hz and above 4000 Hz attenuated least at 13 cm deep (approximately -20 dB), while the upper bound shifted to 2000 Hz at 45 cm deep. Crawford et al. (1997) reported that signals below 400 Hz did not propagate well beyond 0.5 m in a flood plain in the Niger River, West Africa.

Ambient noise levels of near shore marine environments is typically 75 to 85 dB re 1 μPa below 1000 Hz, with velocity levels much higher than the pressure level in shallow water (Banner 1968; Widener 1967). Horch and Salmon (1973) report ambient noise levels in two shallow marine habitats (< 8 m deep) and the graphs indicate levels between 100 and 120 dB re 1 μPa below 1000 Hz. Ambient noise of deep ocean marine environments is typically 65 dB re 1 μPa below 1000 Hz (Coates 1989; Dyer 1998; Wenz 1962). Ambient noise in a flood plain in West Africa was about 40 dB dB re 1 μPa between 200 and 1000 Hz (Crawford et al. 1997). The only published study on ambient noise in streams reported approximately 92 dB re 1 μPa below 1000 Hz during high stream discharge (Stober 1969).

Data presented here document acoustic signal transmission and ambient noise levels in a series of streams around Austin, Texas. Streams differed in levels of surrounding urbanization, and thus hypothetically levels of background noise. Streams also differed in substrate, water depth and current velocity. Ambient noise was quantified and pure tones at frequencies that represent typical fish acoustic signals (50 - 1000 Hz), as well as exemplars of longear sunfish calls, were played back within breeding colonies of longear sunfish (*Lepomis megalotis*, Centrarchidae) to test the hypothesis that lower frequencies transmit better (Zakarauskas 1986) than higher frequencies and that calls transmit better in their stream of origin (Gish & Morton 1981). These data contribute to a small data set for shallow freshwater and may shed light on possible selective forces behind the evolution of acoustic signals in stream animals.

MATERIALS AND METHODS

Ambient noise recordings and playbacks were conducted in five different streams in the Austin, Texas metropolitan area during May - July 2000 between 1100 and 1600 h. All sites except Waller Creek were situated within nature preserves (see Figure 32 in Chapter 5 for map of sites). The Bull Creek site, however, runs parallel to, and in some cases underneath a major highway. The Walnut Metro site is a small metropolitan park surrounded by housing and a busy

street. Waller Creek (WR) runs through the University of Texas at Austin and the site is < 100 m from a power plant. All streams were approximately 5 - 7 m wide with pools 1 - 1.5 m deep and runs 0.25 - 0.5 m deep at mid-stream, with current velocities varying throughout the stream and seasonally. Sites varied in amount of exposed bedrock from Barton Creek with as much as 70% to Onion Creek with < 5%, with other sites averaging 25% exposed bedrock. The thickness and size of gravel covering also varied among sites, although a typical longear sunfish colony had 3 cm diameter gravel at least 7.5 cm deep. Aquatic vegetation was present in substantial quantities only in one part of Bull Creek, and colonies were typically located in unvegetated areas. Water temperatures at 5 cm at the time of data collection ranged from 25.5 to 30.5 ºC.

Ambient noise measurements were calibrated by comparison with tones of known amplitude previously recorded on metal tapes on a Marantz tape recorder (Model # PMD420) at the Applied Research Laboratories of the University of Texas at Austin. All recordings were made within 24 hours of recording the calibration tones and on the same side of the tape using a Benthos hydrophone (Model AQ-20). Signals were digitized using a Turtle Beach Tahiti sound card with no amplitude adjustment. Ambient noise power spectra were calibrated using Spectra Plus (Version 2.3, Sound Technology Inc., 2001) from calibration tones of known amplitude minus amplitude added by hydrophone preamplifier and tape

recorder. Ambient noise was digitized in two minute segments and the power spectra was averaged across the entire segment.

Playback signals consisted of 100 ms pulses of pure tones (50, 75, 100, 125, 150, 175, 200, 225, 250, 300, 350, 400, 450, 500, 600, 700, 800, 900 and 1000 Hz) and two exemplars of fish calls from each site (Figure 25). Exemplars were chosen to represent the average signal for each context (courtship and pursuit) for each site (see Chapter 3 for a discussion of contexts). One courtship and one pursuit call from each site was played at every site. Signals were each played 3 - 5 times through a University Sound UW-30 speaker. The near hydrophone was placed 15 cm from the speaker and the far hydrophone was placed at 50, 100 or 200 cm. A typical longear sunfish nest is 40 cm in diameter and a typical longear sunfish colony is 200 - 300 cm in length and < 200 cm in width. The center of the speaker, the near hydrophone and the far hydrophone (both Benthos AQ-20) were placed at the same depth. Speakers were placed in the center of a sunfish nest within a colony. Sunfish behavior and calls had been recorded previously at each colony. Two transects (the near hydrophone and the three far hydrophone distances) were used at each speaker placement. Typically, one transect ran through the colony and the other away from the colony, but this was not always possible due to stream morphology. All sites, but one, were measured at two colonies for a total of four transects per stream. Hydrophone output was recorded in stereo on the same tape

recorder used for ambient noise recordings with the near and far hydrophones in separate channels.

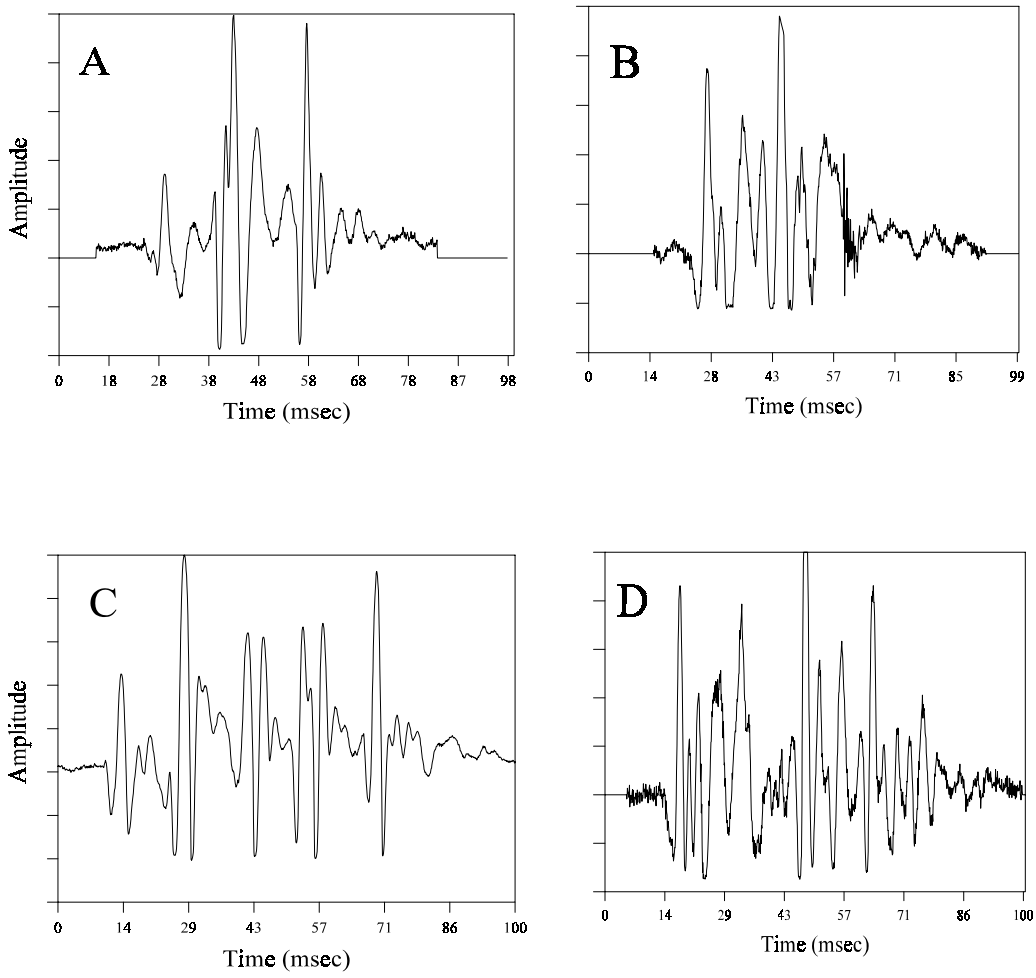

Figure 25. Waveform of fish call exemplars for playback experiments. A, B are from Bull Creek and C, D are from Walnut Creek. A, C are courtship calls and B, D are pursuit calls.

Signals were digitized using a Turtle Beach Tahiti™ sound card with 16 bits and a sample rate of 44,100 samples/sec and analyzed in MATLAB (Version 5.3, Release 11, The Mathworks Inc., 1999). The change over distance for each pulse was measured in four ways, each one comparing the near and far hydrophone output. Two measurements were taken from the waveforms - the cross correlation and the difference in the root mean squares (RMS) between the two hydrophones. In addition, two measurements were taken from the power spectra - the cross correlation (also known as coherence) and the difference in the sound pressure level of the dominant frequency (also known as transmission loss (TL)) between the two hydrophones. The results presented here are averages across all the repetitions for each transect for a given hydrophone distance at each site. Descriptive statistics and Kolmogorov-Smirnov tests were performed in Systat (Version 10, SPSS, Inc., 2000).

RESULTS

Ambient Noise

Ambient noise varied substantially among sites, largely due to changes in surrounding land use (Figure 26). All sites showed significant differences in ambient noise levels when using spectra from 0 - 1000 Hz ($p < 0.001$ except for Walnut and Walnut Metro $p = 0.03$, pair-wise Kolmogorov-Smirnov tests). Waller

(WR) Creek had an average peak sound pressure level (SPL) of 104 dB re 1 μPa at 60 Hz (s.d. = 7.75), with baseline SPL of 83 dB at 100 Hz (s.d. = 5.93) and 56 dB at 1000 Hz (s.d. = 6.35). Bull (BU) Creek had an average peak SPL of 87 dB at 65 Hz (s.d. = 4.61). SPL away from the highway at this site was 84 dB at 100 Hz and 59 dB at 1000 Hz, however, the colony directly underneath a bridge had a peak SPL of 100 dB at 115 Hz, while a more isolated colony had a peak SPL of 83 dB at 115 Hz. Onion (ON), Barton (BA), and Walnut (WT) Creeks are isolated, protected sites with no nearby buildings or busy roads with average peak SPLs of 76 dB at 40 Hz (s.d. = 8.47), 74 dB at 60 Hz (s.d. = 6.29), and 80 dB at 40 Hz (s.d. = 14.46), respectively. Baseline SPLs were 66-71 dB at 100 Hz and 50-53 dB at 1000 Hz. A second site a few miles farther upstream on Walnut Creek (WTM), in a high-use city park with housing and light industry nearby, had a peak SPL of 85 dB at 60 Hz (s.d. = 4.01), but the baseline SPLs were similar to the other Walnut Creek site.

Some statistically significant differences disappeared when using spectra from only 0 - 500 Hz. Onion and Barton had similar spectra and Onion, Walnut and Walnut Metro also resembled one another, but Barton spectra were not similar to either Walnut site. Notably, Waller and Bull, the noisy sites, were not similar to any other sites and showed the greatest statistical differences from other sites (Waller and Bull, $p = 0.016$, pair-wise Kolmogorov-Smirnov).

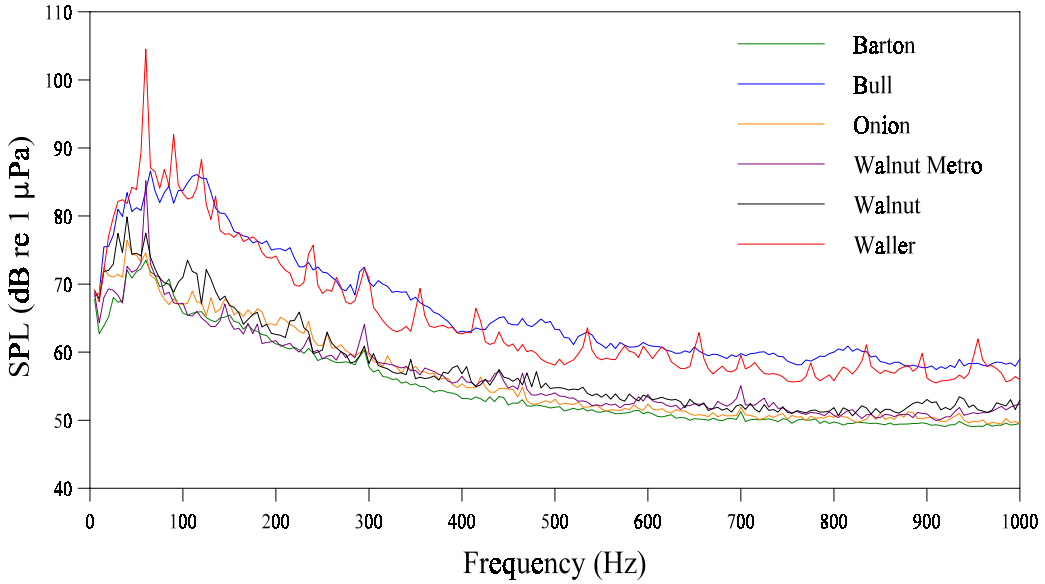

Figure 26. Ambient noise for each site averaged across all recordings. The top two lines are urban sites (WR, BU), while the lower four lines are isolated sites (BA, ON, WT, WTM).

Pure Tones

Expected transmission loss (TL) of pure tones under the assumption of cylindrical spreading from the near hydrophone at 15 cm to the far hydrophones at 50, 100 and 200 cm is -5, -10 and -20 dB respectively (Richardson et al. 1995). Observed TL was approximately -19 dB for 50 cm, -27 dB for 100 cm, and -29 dB for 200 cm for all sites above 200 Hz (Figure 27). For four sites, the frequency with the least TL across all distances was 150 Hz (Table 29). The frequency with the least TL for one transect at the fifth site (ON) varied from 175 Hz at 50 cm, 125

Hz at 100 cm and 150 Hz at 200 cm, while the other transect matched data from other sites. Overall, TL from 200 -1000 Hz was uniform, while TL at 50 Hz was similar to that above 200 Hz (Figure 27). By 200 cm, the signal to noise ratio had decreased to the point where the signal was no longer visible on an oscillogram. The highest coefficient of variation (CV) at each site was at 150 Hz, while the lowest CV was usually at 50 Hz except for one site at 75 Hz and one site that had multiple low CVs above 500 Hz.

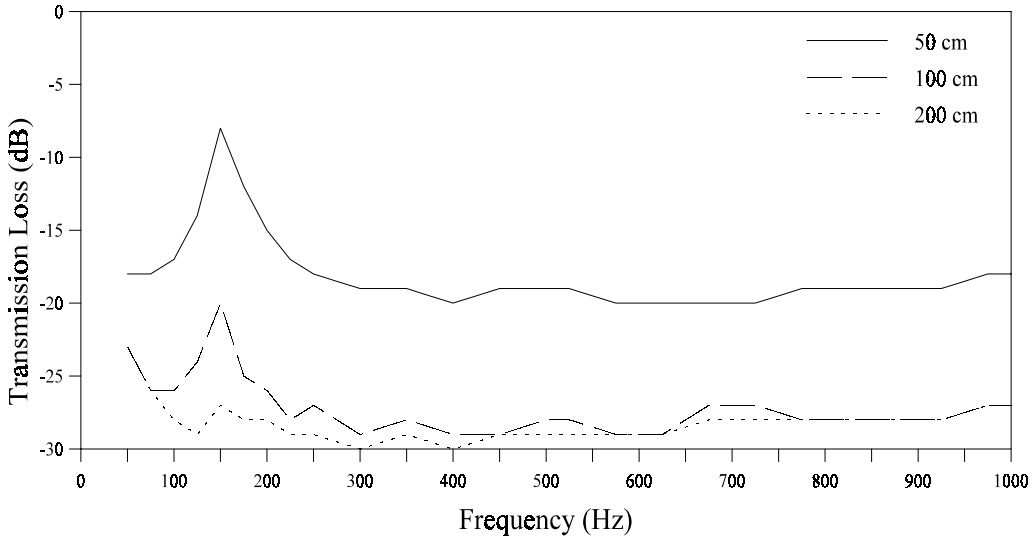

Figure 26. Transmission loss (dB) averaged across all transects and all sites for each hydrophone distance (50, 100 and 200 cm) for each frequency from 50 to 1000 Hz.

Differences in root mean square (RMS), cross-correlation of power spectra, and waveform correlation show a similar pattern with frequencies between 75 and 200 Hz transmitting best (Figure 28). The drop in the cross-correlation of power spectra can be explained by the fact that all the energy is not attenuating equally at the 'best' frequency of 150 Hz. In other words, while the peak attenuated little with distance the rest of the frequencies attenuated greatly changing the shape of the power spectra. The smallest difference in RMS between the near and far hydrophone is also at 150 Hz. The waveform correlation is high from 100 to 500 Hz.

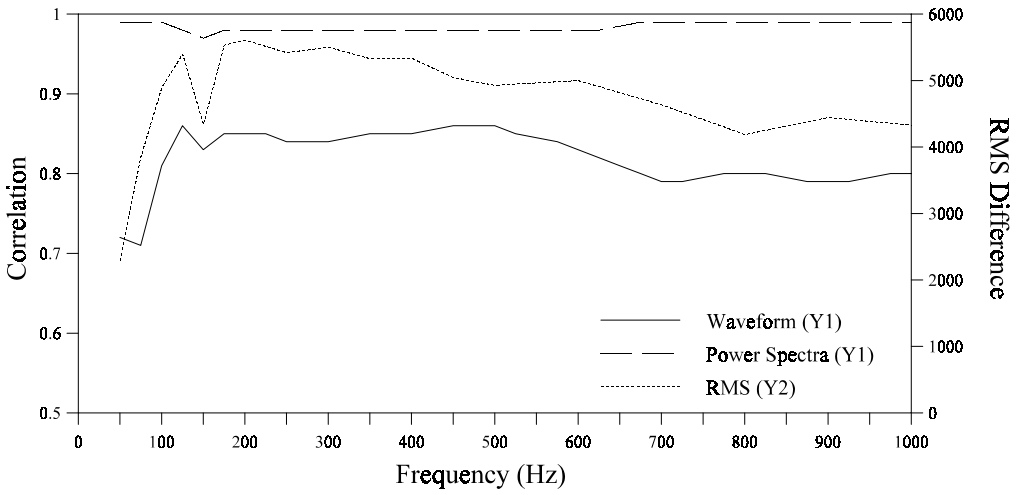

Figure 28. Plot of cross-correlation of waveforms, power spectra and RMS difference for near hydrophone and 50 cm hydrophone averaged across all transects for all sites.

Site	Depth (cm)	Substrate	Best Freq	Excess Attenuation	Average CV
Barton	15-21	Bedrock & Gravel	150	-4 (-11)	0.36 (0.20 - 0.49)
Bull	25-42	Bedrock & Gravel	150	+1 (-6)	0.40 (0.25 - 0.74)
Onion	28-31	Gravel	175	-8 (-19)	0.25 (0.17 - 0.35)
Waller	19-30	Gravel & Bedrock	150	0 (-9)	0.28 (0.19 - 0.56)
Walnut	16-39	Fine Gravel	150	-2 (-12)	0.31 (0.14 - 0.53)

Table 29. Summary of attenuation by site with habitat parameters. Depth is range of depths of speakers for a site. Substrate indicates the substrate underneath the transect, with primary substrate first. Best frequency (Hz) indicates the frequency with the least transmission loss. Excess attenuation (dB) is the SPL decrease beyond theoretical expectations from the near hydrophone to the 50 cm (100 cm) hydrophone. Average CV (Range) is averaged for transmission loss across all transects across all frequencies for each site.

The type and amount of variation is similar across all sites. All sites show the 75 - 200 Hz window, while there are minor variations among sites above 200 Hz (Figure 29). Onion Creek showed the greatest divergence from this pattern as a result of one transect. The coefficients of variation show an almost identical pattern as transmission loss, with 150 Hz showing the greatest amount of variation. Differences among sites for the same distance showed a similar, seemingly random, pattern, with some distances showing significant differences between sites while others did not ($p < 0.001$ to $p = 0.99$, pair-wise Kolmogorov-Smirnov tests). With all data in a nested ANOVA, there were no differences among repetitions ($p = 0.95$) but there were differences among sites, distances, transects and frequencies (all $p < 0.001$).

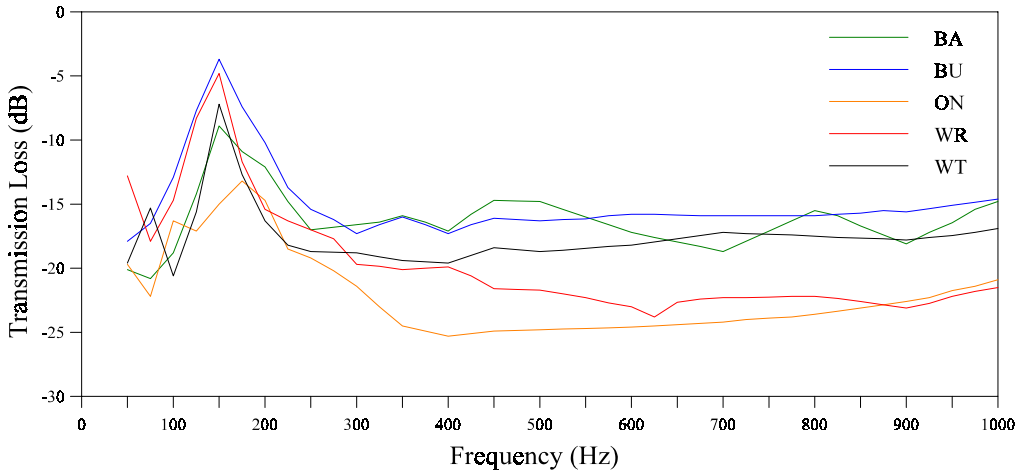

Figure 29. Transmission loss from the near hydrophone to the far hydrophone at 50 cm. Each line represents the average across all transects for each creek.

While the 75 - 200 Hz window was consistent across all transects, there was some within stream variation (Figure 30). As illustrated by Bull Creek in Figure 30, transects within one creek showed variation above 200 Hz, but all transects showed the 75 - 200 Hz window. Only a few significant differences (all statistical tests compared transmission loss data) were found among repetitions at any given distance on any given transect (typically $p > 0.50$, rarely $p < 0.10$ for pair-wise Kolmogorov-Smirnov tests). Statistical differences among transects within a site, however, varied greatly with p-values ranging from $p < 0.001$ to $p = 1.00$ (pair-wise Kolmogorov-Smirnov tests, Table 30). There was no pattern to differences among transects.

Site	50 cm	100 cm	200 cm	Among Transects
Barton	p = 0.52-0.99	p = 0.00-0.99	p = 0.01-0.74	p = 0.00-0.33
Bull	p = 0.01-0.92	p = 0.52-0.99	p = 0.52-0.99	p = 0.00-0.52
Onion	p = 0.05-0.99	p = 0.74-1.00	p = 0.05-1.00	p = 0.00-0.00
Waller	p = 0.20-1.00	p = 0.01-0.92	p = 0.01-0.99	p = 0.00-0.74
Walnut	p = 0.05-0.99	p = 0.05-0.92	p = 0.00-0.52	p = 0.00-0.99

Table 30. Summary of the results for transmission loss. Pair-wise Kolmogorov-Smirnov tests among repetitions for each transect. Among Transects is based on a comparison among transects for 50 cm.

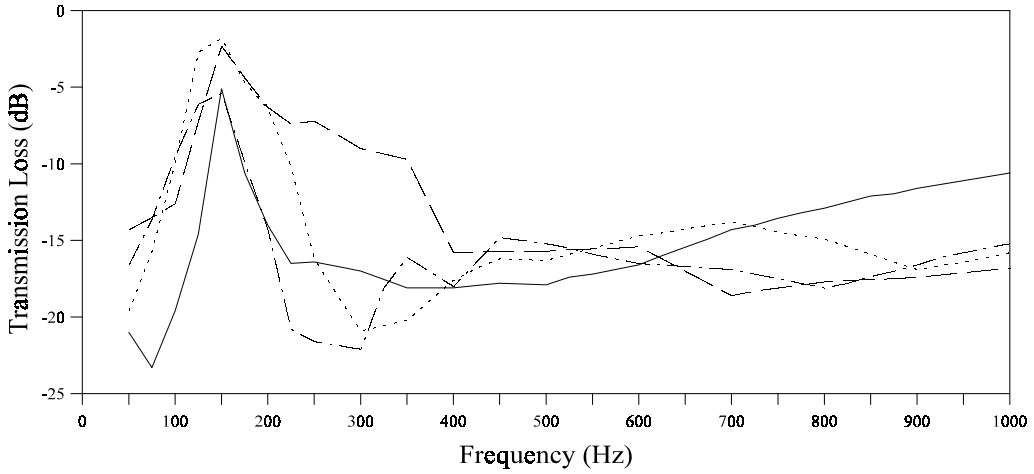

Figure 30. Transmission loss from the near hydrophone to the far hydrophone at 50 cm. Each line represents the averaged data for one transect from Bull Creek.

Fish Calls

While the results for pure tones focused primarily on data from transmission loss, the results for fish calls are based on all parameters. Transmission loss is more difficult to quantify for fish calls because they are broad band and do not have a clearly defined dominant frequency. Overall, there is no obvious pattern in the propagation of fish calls. Based on RMS differences, the Bull (BU) courtship and pursuit calls transmitted better than other calls, while the Onion (ON) pursuit and Walnut (WT) courtship and pursuit calls transmitted worse than the other calls (Figure 31 and see Chapter 3 for differences in contexts). There was no overall difference between pursuit and courtship calls in RMS loss at any distance ($p > 0.30$, two sample t-test), and little additional RMS loss beyond 100 cm. Transmission loss varied from -5 to -12 dB per distance doubling from 50 - 100 cm across sites for both pursuit and courtship calls. There was no additional TL from 100 to 200 cm. Waveform correlations indicate that courtship calls degrade slightly less than pursuit calls ($p = 0.05$, 50 cm only, two sample t-test), but the differences in correlation are slight, approximately 0.80 for courtship calls and 0.78 for pursuit calls. Overall, the courtship calls transmit better, but only *very* slightly. Both courtship and pursuit calls attenuate below the background noise by 100 cm based on RMS differences and TL.

While there was some variation among sites, the pattern at each site was

substantially similar to the overall average pattern (Figure 31). Variation among transects within a site and among sites was similar to that seen with pure tones. There were no observable patterns, either in TL or RMS differences, either within a site or among sites (pair-wise Kolmogorov-Smirnov test, p = 0.00-0.99). Calls did not transmit differently at their site of origin than at the other sites, given that each site showed the same pattern of transmission (Figure 25).

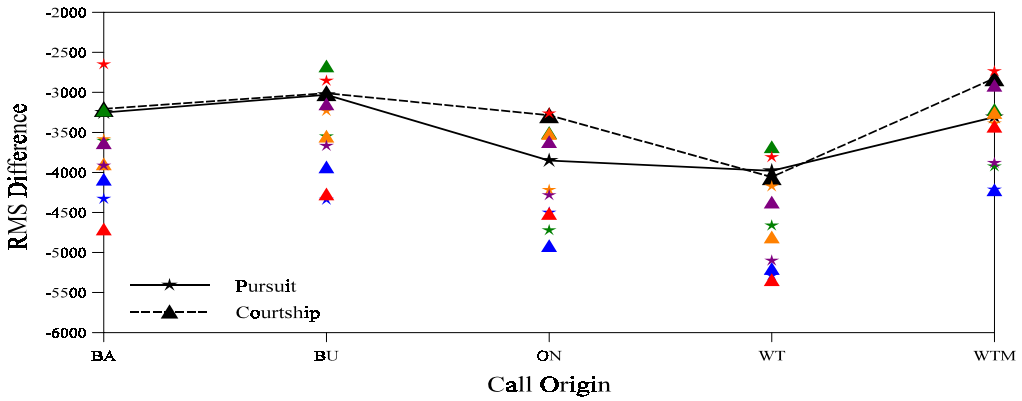

Figure 31. RMS differences in waveforms from the near hydrophone to the far hydrophone at 50 cm. The site abbreviations at the bottom indicate where the exemplar calls originated. The lines indicate the overall average RMS differences for pursuit calls (solid line) and courtship calls (dashed). Stars indicate values for pursuit calls and triangles for courtship calls. Calls indicate site with same legend as other figures in this chapter.

DISCUSSION

Streams in more urbanized areas showed higher levels of background noise than more protected sites. All streams showed a 'window' of best transmission around 150 Hz, in spite of variation in substrate, depth and flow rate. Given the consistency of this window across sites, it is not surprising that many stream fish calls exhibit high energy between 50 and 500 Hz (e.g. Gerald 1971; Takemura 1984; Lugli et al. 1996; Lugli et al. 1997; Johnson 2000; Johnston & Johnson 2000a; Johnston & Johnson 2000b). The previous studies in shallow water, such as Horch and Salmon (1973) and Forrest et al. (1993), found similar but not identical windows.

As acoustic communication of longear sunfish was the motivation for this study, it is interesting to note that the main spectral energy in longear sunfish calls is between 75 and 300 Hz (see Chapter 3 and Gerald 1971) which is above the loudest part of the ambient noise spectra and situated within the window of best transmission. The almost complete attenuation of all signals by 200 cm implies that the signal must be used for short range communication. In other words, the signal is available throughout a typical sunfish colony but not beyond. These findings are similar to those from a flood plain in West Africa for the weakly electric fish *Pollimyrus isidori* (Crawford et al. 1997).

Theoretically, signals over 5000 Hz are experienced by receivers in the far

field in water less than 1 m deep, while signals under 500 Hz are experienced by receivers in the near field (Forrest et al. 1993; Hawkins 1986). Sound transmission in the near field is more complicated and less consistent with greater rates of attenuation than in the far field (Hawkins 1986; Urick 1983). All the data reported here on sound transmission are largely phenomena occurring in the near field. There is a transmission window from 75 and 300 Hz, which contrasts with the 5,500 to 6,000 Hz window reported in Aiken (1982) for shallow streams.

While it is generally acknowledged that low frequency sounds should not propagate well in shallow water, this has not been placed in the context of fish communication. Freshwater fishes appear to have circumnavigated the fact that signals do not propagate well in their habitat by using acoustic signals only for short-range communication, unlike many estuary fish and cetaceans which use acoustic signals for long-range mate attraction (e.g. Bass 1990; Fine 1978; Richardson et al. 1995; Thomas et al. 1992). In fact, the contexts observed during sound production in pond and stream-dwelling fishes may be more similar to fishes living on shallow coral reefs than to other freshwater fishes in estuaries and lakes (e.g. Lobel & Mann 1995; Myrberg 1997).

Freshwater insect signals are typically high frequency, falling between 1,000 - 10,000 Hz, and rely on windows occurring in the far field (Aiken 1982, 1985). Freshwater fish signals are typically low frequency (Johnson 2000; Ladich

1997) and appear to rely on windows occurring in the near field, which can be a few meters for low frequencies in water. In conjunction, pulsed signals are more likely to transmit better underwater than tonal signals (Banner 1971; Richardson et al. 1995), which might contribute to the prevalence of pulsed signals among fishes. Superimposed upon all these phenomena is the fact that frequency information is more likely to degrade and distort in water than is temporal information (Mann & Lobel 1997; Myrberg et al. 1978). This implies that fishes should be more focused on processing of temporal information than spectral information for accurate assessment of the signals and that temporal information might be more constrained, show less variation, and be more species or habitat specific.

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Chapter 5
Geographic Variation in the Acoustic Signals of Longear Sunfish (*Lepomis megalotis aquilensis*)

Calls from longear sunfish collected from five streams around Austin, Texas (*Lepomis megalotis aquilensis*) and from Brier Creek, OK (*L. m. breviceps*) showed significant variation within individuals, among individuals from the same population, among populations of the same subspecies and between subspecies. These differences were expressed in both pursuit and courtship calls. Courtship calls are more distinctive than pursuit calls among sites within one watershed. Microgeographic variation in acoustic signals as documented here has not been previously reported in fishes. This study describes variation in a communication system at every level within a species and provides insight into how this variation plays a role in geographic divergence and evolution in longear sunfish.

INTRODUCTION

Geographic variation in a communication system, or other behavior, can be caused by variation in habitat, pleiotropic effects with other non-behavioral characters, genetic drift, and selection due to interactions between species (e.g. reproductive character displacement) and among conspecifics that vary geographically (e.g. female mate choice) (Foster 1999; Wilczynski & Ryan 1999).

Although geographic variation in song dialects in birds has been well-studied (e.g. Nottebohm 1975), the learning of songs results in complex and unpredictable associations among song components, habitat, gene flow, migration and sexual selection.

Calls in frogs are also well-studied and exhibit geographic variation. In cricket frogs (*Acris crepitans*), many call parameters, as well as the auditory system, vary along a cline though female preference does not (Wilczynski & Ryan 1999). Several selective forces drive this variation. Body size has a pleiotropic effect on dominant frequency and auditory tuning, with larger frogs in the western populations having lower dominant frequencies and being tuned to lower frequencies. Different selection on signal design occurred depending on habitat. Given the diversity of habitat in freshwater systems, comparable complexity in selection forces would be expected. The lack of knowledge about acoustic communication and transmission in freshwater make it difficult to predict how selection will act in a given habitat.

While geographic variation in bird song and frog calls has been well documented (Littlejohn 1999; Ryan et al. 1996; Wilczynski & Ryan 1999), few studies examine geographic variation in the calls of marine or freshwater fishes (Fine 1978a,b; Mann and Lobel 1998). An inconclusive study by Fine (1978a,b) found small, possibly non-significant, geographic differences in acoustic signals of

the estuarine oyster toadfish *(Opsanus tau)*. The single comprehensive study by Mann & Lobel (1998) found no difference in acoustic signals of the marine domino damselfish (*Dascyllus albisella*) between the Johnston Atoll and Hawaii, which are 1000 km apart. This parallels the relative lack of variation in morphology, color and genes in marine fish. Freshwater fish, however, typically have substantial variation in morphology, color patterns, and behavior (Ehlinger 1999; Endler 1995; Fox et al. 1997; Hernandez-Martich & Smith 1990; Magurran 1999; Matthews 1995; Robinson et al. 1993; Warren 1992; Winemiller et al. 1990), so similar amounts of variation in acoustic signals might be expected. To date intraspecific geographic differences in acoustic signals in freshwater fishes have not been studied.

Sunfish present one system in which to study microevolution and speciation through geographic variation in acoustic communication, as they meet many of the criteria presented by Endler (1995), such as known ecology, partially known genetic variation, measurable geographic variation, two or more geographically and geologically stable habitats, geographical ranges larger than gene flow scale. Thorough descriptions of genetic variation within individual *Lepomis* species are lacking, however, there are several studies that focus on a small region with a few token specimens from other regions (Avise & Smith 1974; Dillman et al. 2000; Fox et al. 1997; Jennings & Philipp 1992; Warren 1992). These studies, though

incomplete, consistently demonstrate genetic differences among geographic regions although magnitude varies. In addition, Barlow (1980) discusses in detail the morphological variation in *Lepomis megalotis* and concludes that there are at least seven subspecies. These data support the theory of widespread and substantial geographic variation in *Lepomis megalotis*, at least for morphology and genes.

Gerald (1971) reported on species-specific courtship signals in *Lepomis* species. Variation among species is obviously important for understanding the evolution of communication and reproduction, but there are also important patterns of variation among populations within a species, among individuals within a population, and within an individual. The variation within an individual provides clues as to the morphological constraints in the production mechanism as well as the strength of selection for a stereotyped signal (Ryan 1988). Variation among individuals allows for the possibility of individual recognition (Butlin 1995; Hauser 1996). Variation among sites indicates how specific the signals are to the species versus the population and describes the potential for population divergence and speciation (Endler 1995; Foster 1999; Magurran 1999; Matthews 1995; Thompson et al. 1997; Wilczynski & Ryan 1999).

My study describes variation in acoustic signals of *Lepomis megalotis aquilensis* within an individual, among individuals within a site, and among sites, with a preliminary comparison to *L. m. breviceps*. Call parameters are compared

across levels to discern patterns of variation at each level and how that variation might influence the structure of longear sunfish calls. Finally, possible selective forces, such as habitat and gene flow, driving this variation are discussed. Substantial variation is expected at each level, with no expectation as to which call parameters will vary most. Habitat differences due to environmental selection and geographic distance related to genetic isolation are expected to explain some of the variation in acoustic signals.

MATERIALS AND METHODS

Calls of parental male longear sunfish (*Lepomis megalotis*, Family Centrarchidae) were studied in clear, shallow streams in Austin, Texas (Figure 32) from May to August in 1998, 1999, and 2000. In addition, parental males were recorded from Brier Creek, Oklahoma in May 1999 and Cuatro Ciénegas, Coahuila, México in August 1999. Synchronized video and audio recordings were made on Hi-8 metal particle videotapes using a Benthos AQ-20 hydrophone and a Hitachi VMH-100LA videocamera. The submersible lens and hydrophone were placed on the edge of the nest and recordings began when the male was acclimated, typically in less than 15 minutes. Males were considered acclimated when they resumed patrol and defense activities.

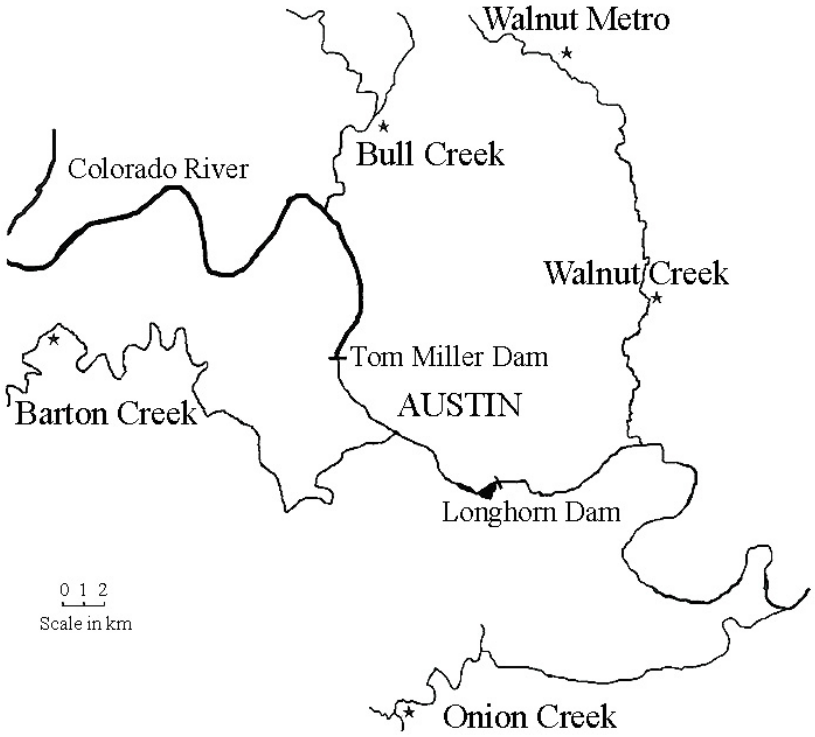

Figure 32. Map of study sites around Austin, Texas. Waller Creek would be in the middle of 'Austin".

I digitized calls from Hi-8 tape onto an IBM-PC computer using a Turtle Beach Tahiti sound card. I performed signal analysis in MATLAB (Version 5.3, Release 11, The Mathworks Inc, 1999) using damped sinusoid discrete wavelet transforms (see Chapter 2 for details). I measured fourteen call parameters, both temporal and spectral (see Figures 7 and 6 and Table 3 in Chapter 2). Dominant frequency (*Freq 1*) is the mode with the most energy. Second frequency (*Freq 2*) is the mode with the second highest energy. Mean frequency (*Mean Freq*) is the

weighted mean frequency calculated from each mode for a pulse weighted by its relative energy. Minimum frequency (*Min Freq*) is the mode with the lowest frequency, while maximum frequency (*Max Freq*) is the mode with the highest frequency. Pulse duration (*P Dur*) is the time difference between the first mode and the last mode, or the duration of the longest mode. *Rise time* is the time difference between the first mode and the dominant frequency mode. *Fall time* is the time difference between the last mode and dominant frequency mode. Duration 1 (*Dur 1*) is the duration of the dominant mode. Duration 2 (*Dur 2*) is the duration of the second mode. Inter-pulse interval (*IPI*) is the time difference between the last mode of the first pulse and the first mode of the next pulse. Pulse rate (*P Rate*) for calls with more than 1 pulse was calculated as number of pulses/call duration. For calls with only one pulse, pulse rate was arbitrarily set to 1. Call duration (*Call*) is the time difference between the first mode of a call and the last mode of the call. All analyses were performed using data averaged across pulses for a single call and also using each pulse separately. This allows for the substantial variability in number of pulses in a call (especially courtship calls) and substantial variability in spectral and temporal information among pulses in the same call.

Descriptive and analytical statistics were performed in Systat (Version 10, SPSS Inc, 2000.). Transformed data were used in all statistical analyses. Frequency data were transformed using $\sqrt{x + \frac{3}{8}}$, while time data were transformed

using $\sqrt{x} + \sqrt{x+1}$ following Zar (1999) for Poisson distributions. Descriptive statistics used all the call parameters, but analytical statistics did not use duration 1, duration 2, second frequency or frequency span. These parameters were excluded to increase statistical power as they were highly correlated with other call parameters (see Correlations, Chapter 3). Courtship calls and pursuit calls were always analyzed separately (see Chapter 3 for differences between contexts). Rankings of coefficients of variation (CV) were generated from lowest CV to highest for each parameter and each level of analysis. Comparisons of rankings were done with the Friedman test statistic and Kendall's coefficient of coherence (Zar 1999). Comparisons were made with ANOVA and MANOVA using nested data when appropriate. Intra- and inter-site comparisons were performed three ways: 1) with every pulse from the male included in the data set or 2) with randomly selected pulses from each male included or 3) with pulses for a given call averaged and the call as the unit of analysis. Intra-individual and intra-site data sets included only males with at least fifteen pulses per context or at least nine calls per context. The microgeographic data set (within Austin area) included only males with at least ten pulses per context or with at least four calls per context. Since only 7 - 9 pulses were recorded from many of the males from Oklahoma and México, the macrogeographic data set (Austin, Oklahoma and México) included males with at least five pulses per context or at least four calls per context.

Site	≥ 15 pulses	≥ 10 pulses	≥ 5 pulses
Barton	9 Total 7 Courtship 6 Pursuit	13 Total 7 Courtship 7 Pursuit	20 Total 8 Courtship 13 Pursuit
Bull	17 Total 10 Courtship 7 Pursuit	19 Total 10 Courtship12 Pursuit	20 Total 10 Courtship15 Pursuit
Onion	3 Total 3 Courtship 1 Pursuit	9 Total 6 Courtship 4 Pursuit	14 Total 6 Courtship 10 Pursuit
Waller Campus	1 Total 0 Courtship 1 Pursuit	5 Total 1 Courtship 4 Pursuit	12 Total 1 Courtship 11 Pursuit
Walnut Metro	9 Total 6 Courtship 3 Pursuit	13 Total 8 Courtship 6 Pursuit	19 Total 8 Courtship 12 Pursuit
Walnut	13 Total 5 Courtship 8 Pursuit	14 Total 5 Courtship 13 Pursuit	21 Total 8 Courtship 20 Pursuit
Okla-homa	2 Total 1 Courtship 1 Pursuit	2 Total 1 Courtship 1 Pursuit	6 Total 1 Courtship 5 Pursuit
México	1 Total 0 Courtship 1 Pursuit	1 Total 0 Courtship 1 Pursuit	2 Total 0 Courtship 2 Pursuit
Total	55 Total 32 Courtship 28 Pursuit	76 Total 38 Courtship 48 Pursuit	112 Total 42Courtship 87 Pursuit

Table 31. Number of males per site with indicated number of pulses for courtship and pursuit calls.

Correlations were generated using Pearson's correlation coefficients, significance values were $\alpha = 0.05$ with Bonferroni corrections for multiple comparisons. Tests for differences among groups were conducted with MANOVA tests using pulses and with multiple ANOVA tests using call averages. ANOVA tests within individuals and among individuals within a site were not nested. The " level was adjusted for these multiple tests using the Dunn-Šidák correction (Zar

1999). Males were nested within site for within stream and microgeographic analyses, and males were nested within site nested within subspecies for the macrogeographic analyses. The Mantel test in microgeographic variation was performed in Mantel non-parametric test calculator (Version 2.0, Adam Liedloff, 1999). Principal components analyses (PCA) were used to examine the variation within sites and determine which parameters contributed most to the variation. In addition, discriminant function analyses (DFA) were used at each level to explore which parameters were useful for categorizing at a given level.

RESULTS

Analyses of within and among male variation used data from males with ≥ 15 pulses or > 8 calls per context. Within stream and microgeographic (inter-site) analyses used males with ≥ 10 pulses or > 4 calls per context. Macrogeographic (subspecies) analyses used males with ≥ 5 pulses or > 4 calls per context.

Within Individual

I assessed variation among calls from a given male by comparing coefficients of variation (CV) in a data set limited to males with ≥ 15 pulses per context (28 males with pursuit calls, 32 with courtship calls) or > 8 calls per context (35 pursuit, 14 courtship).

		CV		Range		Rank	
	Parameter	**Pursuit**	**Court**	**Pursuit**	**Court**	**Pursuit**	**Court**
Least	Duration 1 (msec)	0.06	0.05	87	63	2	2
	Duration 2 (msec)	0.05	0.05	46	45	1	3
	Pulse Duration (msec)	0.07	0.05	132	98	3	1
	Rise Time (msec)	0.07	0.07	73	66	3	5
	Fall Time (msec)	0.07	0.06	103	72	5	4
	IPI (msec)	0.23	0.16	639	977	7	8
	Mean Freq (Hz)	0.23	0.10	457	208	8	6
	Maximum Freq (Hz)	0.21	0.13	699	435	6	7
	Call Duration (msec)	0.23	0.37	1,730	9,880	9	13
Greatest	Minimum Freq (Hz)	0.39	0.31	283	225	12	12
	Dominant Freq (Hz)	0.33	0.16	558	270	11	9
	Second F (Hz)	0.33	0.20	597	370	10	10
	Freq Span (Hz)	0.36	0.29	816	574	13	11
	Pulse rate (pulses/sec)	0.52	0.23	48.0	6.67	14	14

Table 32. Summary of CV and ranks from transformed data averaged across all males. Summary of average ranges measured from untransformed data. Ranks from least to most variable. The lines indicate groups with similar amounts of variation. Each statistic based on an average across all males' individual rankings.

As in Table 32 and discussed in Chapter 3, ranges and CVs for courtship calls were smaller than for pursuit calls, except for pulse rate. Overall rankings of CVs for pursuit and courtship calls share some similarities (Table 32). In both contexts, pulse duration, duration 1 and duration 2 were least variable. Dominant, second, and minimum frequency, frequency span, and pulse rate were most

variable. Inter-pulse interval, mean and maximum frequency and call duration exhibited intermediate variability.

Among Individuals (Intra-Site)

Differences among males within a population were examined using the same data set as in the previous section (males with ≥ 15 pulses per context or > 8 calls per context). Due to a limited number of males with ≥ 15 pulses per context, only Barton (BA), Bull (BU), Walnut (WT) and Walnut Metro (WTM) are examined. The males within each site were significantly different from each other for most call parameters, with the exception of pulse rate (Table 33). There were significant differences among males regardless of whether data were averaged for a call or if every pulse per male was analyzed or whether analysis was performed with MANOVA or multiple ANOVAs with correction for multiple tests (see Table 33 for results). Pulse duration, mean frequency, minimum frequency, and dominant frequency show consistent differences among individuals at almost every site. Pulse rate, however, had no significant differences among males. Call duration, rise time and fall time do not show consistent patterns among sites.

	Pursuit				Courtship		
Site	BA	BU	WT	WTM	BA	BU	WT
# Males	7	12	11	5	4	4	7
Pulse Duration	0.04	**0.000**	**0.000**	0.02	**0.000**	**0.000**	**0.006**
Rise Time	0.01	0.18	0.04	**0.006**	**0.000**	0.15	0.54
Fall Time	0.40	0.04	**0.000**	0.52	0.02	**0.000**	**0.001**
Mean Frequency	**0.001**	0.01	**0.000**	**0.000**	**0.000**	**0.000**	**0.000**
Maximum Frequency	0.14	**0.000**	**0.000**	0.15	**0.004**	0.01	**0.000**
Call Duration	0.03	0.64	**0.000**	0.80	0.01	**0.000**	0.02
Minimum Frequency	0.03	**0.000**	**0.000**	**0.001**	0.22	**0.000**	0.12
Dominant Frequency	**0.001**	0.06	**0.000**	0.02	**0.000**	**0.000**	**0.000**
Pulse Rate	0.30	0.01	0.08	0.61	0.02	0.33	0.04
MANOVA	**0.013**	**0.000**	**0.000**	**0.000**	**0.000**	**0.000**	**0.000**

Table 33. Intra-site probabilities from ANOVA using call averages for each individual within a site. Significant p-values ($\alpha = 0.006$ based on Dunn-Šidák correction) in bold. MANOVA results based on pulses instead of call averages with $\alpha = 0.05$.

Pulse duration shows little variability within a male but is most variable of temporal parameters among males (Table 34). CVs for temporal parameters were typically below 0.05, except for call duration and pulse rate which were between 0.09 and 0.26. CVs for spectral parameters were typically between 0.05 and 0.30.

Parameter	Pursuit CV	Courtship CV	Pursuit Rank	Courtship Rank
Duration 1	0.02	0.02	*1*	*2*
Duration 2	0.02	0.01	*1*	*1*
Pulse Duration	0.04	0.03	*5*	*4*
Rise Time	0.03	0.02	*3*	*3*
Fall Time	0.03	0.03	*4*	*4*
Mean Frequency	0.13	0.06	*8*	*6*
Maximum Frequency	0.10	0.15	*6*	*10*
Call Duration	0.10	0.13	*7*	*7*
Minimum Frequency	0.19	0.29	*12*	*14*
Dominant Frequency	0.15	0.16	*10*	*11*
Second Frequency	0.15	0.18	*11*	*12*
Frequency Span	0.14	0.14	*9*	*8*
Pulse Rate	0.21	0.19	*13*	*13*

Table 34. Coefficients of variation and rankings for intra-site variation in pursuit and courtship calls. The CV is based on averages for each male within a site. The CV ranking is from lowest to highest.

Due to the large number of call parameters, principal components analyses (PCA) on transformed data were used to determine which parameters explain the variation (Zar 1999). There was substantial variability in PCA loadings, with the first factor explaining 40% and the second factor explaining 22% on average for both pursuit and courtship calls. For pursuit calls, mean, dominant and maximum frequency and pulse duration were important in PCA loadings (Table 35). For courtship calls, mean, dominant and maximum frequency were important in PCA

loadings. In other words, courtship calls exhibit less variability in temporal parameters than pursuit calls, but similar variability in spectral parameters.

	Pursuit				Courtship		
Site	BA	BU	WT	WTM	BA	BU	WT
# Males	7	12	11	5	4	4	7
Pulse Duration	0.63	-0.64	-0.40	-0.69	0.38	0.15	0.07
Rise Time	0.27				0.82	0.01	0.48
Fall Time	0.64				0.10	0.38	-0.19
Mean Frequency	0.82	0.92	0.95	0.88	0.86	-0.90	0.91
Maximum Frequency	-0.57	0.38	0.58	0.45	0.64	-0.67	0.48
Call Duration	0.45	-0.18	0.23	-0.08	-0.15	0.57	0.20
Minimum Frequency	-0.67	0.64	0.78	0.61	0.29	0.24	0.54
Dominant Frequency	-0.74	0.88	0.89	0.86	0.88	-0.87	0.93
Pulse Rate	0.04	0.13	0.32	0.37	0.38	0.45	0.04
% Variance	34	38	42	38	37	30	28

Table 35. Factor loadings among males within a site for first factor from PCA based on call averages only. Empty cells indicate parameters not included in analysis.

Discriminant function loadings from a backwards stepwise DFA were used to explore groupings of parameters that helped classify calls by individual using both pulses and call averages. Within a site, correct classifications of pursuit calls to individuals ranged from 30 - 53% (random expectation = 13 - 33%) regardless of data set. Mean, minimum, and maximum frequency and pulse duration were

important in this classification (Table 36). Within a site, correct classifications of courtship calls to individuals ranged from 47 - 88% (random expectation = 10-33%). Mean and maximum frequency, pulse duration and call duration were important in this classification (Table 36). There were some differences between call averages and individual pulses, but the trends were substantially the same. Although pulse duration is not the most variable parameter in courtship calls, it is extremely important in distinguishing among males within a site.

	Pursuit				**Courtship**		
Site	BA	BU	WT	WTM	BA	BU	WT
# Males	7	12	11	5	4	4	7
Pulse Duration	1.27	1.47	0.18		4.87	-2.23	0.48
Rise Time		-0.65		-0.62	-7.07	2.06	
Fall Time	-1.02	-0.55			-6.30	1.45	
Mean Frequency	1.04	0.11		0.53	-0.53	-1.76	0.90
Maximum Frequency	-0.77	-0.15	0.44		2.22	0.38	-0.40
Call Duration			0.60		0.60	-0.12	0.52
Minimum Frequency		-0.77	0.72	0.49	1.53	1.24	-0.40
Dominant Frequency		0.18			0.97	0.29	
Pulse Rate	-0.37			-0.25		-0.12	-0.43
% Random	14	8	9	20	25	25	14
% Correct	33	39	29	46	82	87	59

Table 36. Factor loadings for classifying males within a site from the first function in DFA based on call averages. Empty cells indicate parameters removed during stepwise DFA.

Within Stream (Walnut Creek)

To determine if calls from the two sites within the Walnut Creek watershed were different, an expanded data set (including males with ≥ 10 pulses per context or > 4 calls per context: 8 males with courtship calls and 6 with pursuit calls for Walnut Metro and 5 males with courtship calls and 13 with pursuit calls for Walnut) was examined. Pursuit calls and courtship calls from Walnut and Walnut Metro were significantly different in analyses using either call averages (Table 37), all pulses per male or 10 exemplars per male. Rise time and pulse rate were not significantly different between Walnut and Walnut Metro for either pursuit or courtship calls, while call duration was not different for pursuit calls and minimum frequency was not different for courtship calls.

DFA was used to classify calls to site using call averages, all pulses per male and only 10 pulses per male. For pursuit calls, pulse duration, fall time, rise time, mean frequency, and minimum frequency were important for classification by site regardless of data set (Table 37). DFA classified 59% of pursuit calls correctly using call averages, but only 39 - 43% correctly using the pulses (random expectation = 50%). In other words, it was difficult to classify pursuit calls to the correct site, but slightly easier using call averages than individual pulses. For courtship calls, pulse duration, call duration and pulse rate as well as all the frequency parameters were important for classification (Table 37) regardless of data

set. DFA classified 87% of courtship calls correctly using call averages, but only 60 - 68% correctly using pulses (random expectation = 50%).

Call Parameter	Pursuit ANOVA	Courtship ANOVA	Pursuit DFA	Courtship DFA
Pulse Duration (msec)	**0.000**	**0.000**	2.65	0.45
Rise Time (msec)	0.01	0.01	-1.30	
Fall Time (msec)	**0.001**	**0.000**	-2.41	
Mean Frequency (Hz)	**0.000**	**0.000**	0.74	-0.41
Maximum Frequency (Hz)	**0.000**	**0.000**		0.58
Call Duration (msec)	0.02	**0.003**		0.68
Minimum Frequency (Hz)	**0.000**	0.03	-0.71	-0.59
Dominant Frequency (Hz)	**0.000**	**0.000**		0.34
Pulse Rate (pulses/sec)	0.42	0.02		-0.34
Nested MANOVA	**0.000**	**0.000**	n/a	n/a

Table 37. Probabilities for Walnut Creek differences from nested ANOVAs based on call averages. Significant p-values ($\alpha = 0.006$ Dunn-Šidák correction) in **bold**. MANOVA results based on pulses with $\alpha = 0.05$. Factor loadings for the first factor from DFA based on call averages for classifying Walnut vs. Walnut Metro. Empty cells indicate parameters removed during stepwise DFA.

Microgeographic (Inter-Site)

Differences among calls from all sites within the Colorado River drainage were compared (Barton, Bull, Walnut, Walnut Metro, Onion, and Waller) using the same data as in the previous section (males with ≥ 10 pulses per context or > 4 calls

per context). For both contexts, calls from each creek were significantly different from each other regardless of data set (i.e., call averages, all pulses/male or 10 pulses/male). For courtship calls, all parameters were significantly different among sites, while for pursuit calls all parameters except pulse rate were significantly different among sites (Table 38). Individual ANOVA tests using call averages and MANOVA tests using pulses were based on a nested design with individuals nested within site.

Call Parameter	Pursuit ANOVA	Courtship ANOVA	Pursuit DFA	Courtship DFA
Pulse Duration (msec)	**0.000**	**0.000**	1.10	1.20
Rise Time (msec)	**0.000**	**0.000**		-0.49
Fall Time (msec)	**0.000**	**0.000**	-0.46	-0.39
Mean Frequency (Hz)	**0.000**	**0.000**	0.64	-0.67
Maximum Frequency (Hz)	**0.000**	**0.000**	-0.65	0.59
Call Duration (msec)	**0.003**	**0.000**	-0.14	
Minimum Frequency (Hz)	**0.000**	**0.000**	-0.61	-0.32
Dominant Frequency (Hz)	**0.000**	**0.000**		0.11
Pulse Rate (pulses/sec)	0.19	**0.000**		0.16
Nested MANOVA	**0.000**	**0.000**	n/a	n/a

Table 38. Probabilities from inter-site differences from nested ANOVAs based on call averages. Significant p-values ($\alpha = 0.006$ Dunn-Šidák correction) in **bold** (n = 73 pursuit males, n = 30 courtship males). MANOVA results based on pulses with $\alpha = 0.05$ (n = 46 pursuit males, n = 36 courtship males). Factor loadings for the first factor from DFA based on call averages for classifying to site. Empty cells indicate parameters removed during stepwise DFA.

Step-wise DFA was used to classify calls to site using call averages, all pulses per male and only 10 pulses per male. Pulse duration was the most important parameter for distinguishing among sites for both courtship and pursuit calls. For pursuit calls, all call parameters except rise time, pulse rate and dominant frequency were important for classification by site (Table 37) regardless of data set. DFA classified 21 - 28% of pursuit calls correctly regardless of data set (random expectation = 17%). Waller pursuit calls were classified ~51% correctly, while Barton, Bull and Onion pursuit calls were classified 26 - 37% correctly. Walnut and Walnut Metro were correctly classified only ~15% of the time, however, if Walnut and Walnut Metro were lumped together, they were classified correctly 40% of the time. For courtship calls, all call parameters were important for classification regardless of data set and DFA classified 45 - 57% of courtship calls correctly (random expectation = 20%). Waller and Walnut Metro courtship calls were classified 70% correctly, Onion 65% correctly and Barton, Bull and Walnut were classified ~50% correctly. There was no relationship between geographic distance and pulse duration among sites (Mantel test, $g = -0.89$ courtship, $g = -1.09$ pursuit) or mean frequency (Mantel test, $g = 1.20$ courtship, $g = -1.12$ pursuit; a g-statistic < 1.65 indicates that there is no association with geographic distance). In other words, greater differences in pulse duration or mean frequency were not associated with greater distance.

Figures 33 and 34 are plots of scores for the first two factors in the PCA from Chapter 3, but coded for site instead of context (see Figure 24 in Chapter 3). Pursuit calls overlap substantially more than courtship calls. The courtship calls tend to cluster for each site, while the pursuit calls are more evenly scattered.

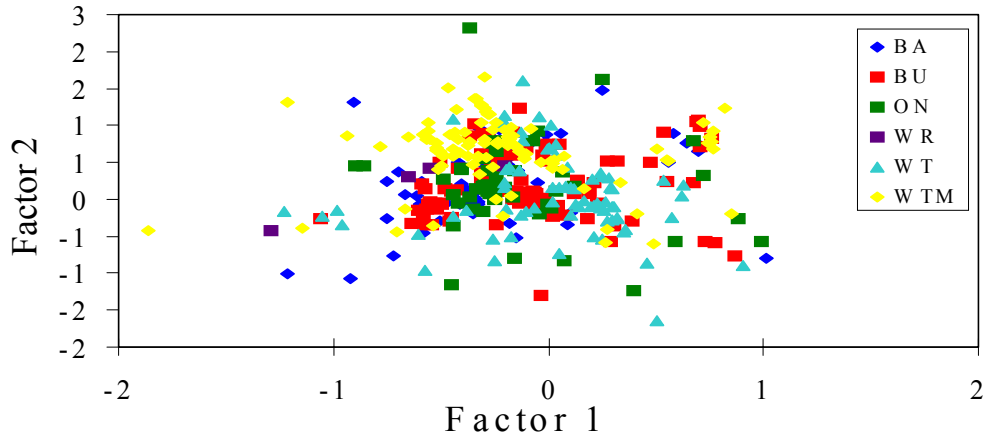

Figure 33. Results from PCA for all courtship calls coded by site. Note the difference in scale compared to pursuit calls.

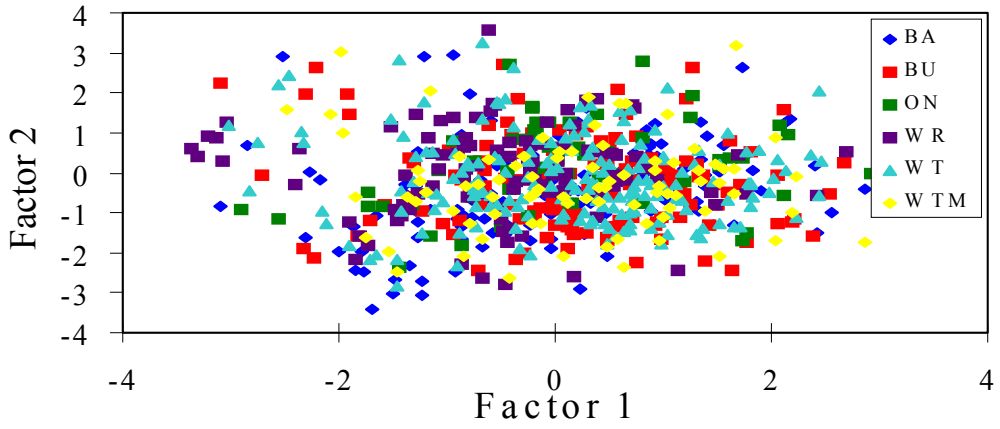

Figure 34. Results from PCA for all pursuit calls coded by site.

Figures 35 and 36 are plots of scores for the first two factors in the DFA based on site for courtship and pursuit calls. Courtship calls overlap less among sites than do pursuit calls. Walnut and Walnut Metro overlap completely for courtship and pursuit calls, while Barton and Onion overlap less with the central cloud of data for courtship calls.

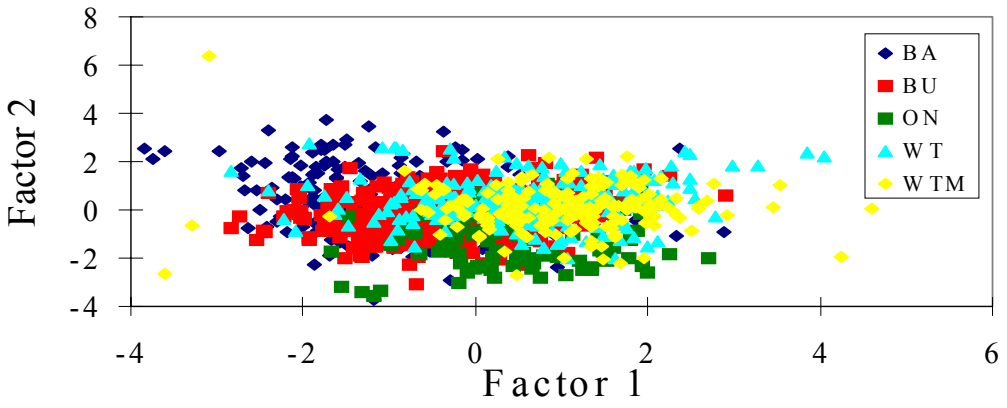

Figure 36. Results from DFA for microgeographic (inter-site) classification of courtship calls. Note the difference in scale from pursuit calls.

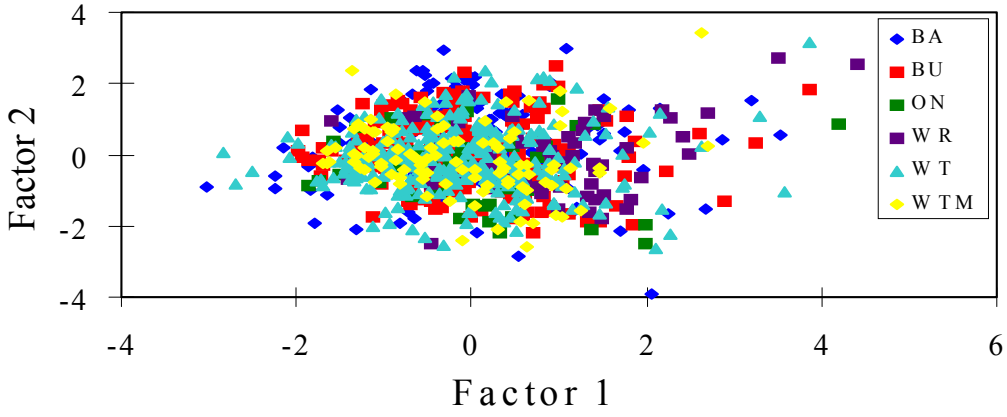

Figure 35. Results from DFA for microgeographic (inter-site) classification of pursuit calls.

Tables 39 and 40 present summaries by site of both courtship and pursuit calls for each call parameter. Of particular note are high duration 1, pulse duration and rise time and low dominant frequency, second frequency, mean frequency, minimum frequency and frequency span for courtship calls from Waller Creek (WR), possibly as a result of noise pollution. Also of note is the high minimum frequency, maximum frequency, and frequency span for courtship calls from Barton Creek (BA), possibly due to smaller body size.

Call Parameter	**BA**	**BU**	**ON**	**WR**	**WT**	**WTM**
Duration 1 (msec)	22	19	24	28	18	17
Duration 2 (msec)	10	11	12	14	12	12
Pulse Duration (msec)	36	33	41	59	37	35
Rise Time (msec)	13	12	15	23	15	13
Fall Time (msec)	22	21	22	35	23	20
Inter-pulse Interval (msec)	215	266	249	220	355	248
Mean Frequency (Hz)	223	228	214	199	249	239
Maximum Frequency (Hz)	495	495	535	435	518	494
Call Duration (msec)	123	154	134	113	230	145
Minimum Frequency (Hz)	90	93	76	59	95	89
Dominant Frequency (Hz)	209	216	192	193	235	230
Second Frequency (Hz)	242	240	256	197	258	235
Frequency Span (Hz)	392	378	430	372	394	391
Pulse Rate (pulses/sec)	3.84	4.50	3.19	2.69	3.67	4.88

Table 39. Averages for each call parameter for each site for pursuit calls.

Call Parameter	BA	BU	ON	WR	WT	WTM
Duration 1 (msec)	22	20	29	36	24	29
Duration 2 (msec)	11	12	19	15	15	18
Pulse Duration (msec)	36	40	52	64	50	60
Rise Time (msec)	14	13	15	30	17	22
Fall Time (msec)	21	27	36	33	33	38
Inter-pulse Interval (msec)	372	374	422	418	466	556
Mean Frequency (Hz)	253	231	176	163	253	227
Maximum Frequency (Hz)	482	415	366	308	417	406
Call Duration (msec)	1,409	1,920	989	1,368	1,898	1,335
Minimum Frequency (Hz)	125	105	62	77	112	85
Dominant Frequency (Hz)	221	218	173	163	253	214
Second Frequency (Hz)	283	240	174	174	253	235
Frequency Span (Hz)	341	304	287	216	300	314
Pulse Rate (pulses/sec)	3.01	2.68	2.61	2.49	2.25	2.28

Table 40. Averages for each call parameter for each site for courtship calls.

Duration 2 is again the least variable parameter in this analysis, as it was within sites. Dominant frequency, minimum frequency, second frequency, and pulse rate are again the most variable parameters (Table 41 and Table 43) as in previous sections.

Parameter	CV Pursuit	CV Courtship	Rank Pursuit	Rank Courtship
Duration 1	0.01	0.02	3	2
Duration 2	0.00	0.01	1	1
Pulse Duration	0.02	0.03	4	4
Rise Time	0.02	0.03	5	4
Fall Time	0.01	0.02	2	2
Mean Frequency	0.04	0.11	8	11
Maximum Frequency	0.03	0.08	6	8
Call Duration	0.03	0.11	7	11
Minimum Frequency	0.09	0.12	12	13
Dominant Frequency	0.05	0.11	11	11
Second Frequency	0.05	0.10	10	10
Frequency Span	0.05	0.09	9	9
Pulse Rate	0.14	0.06	13	7

Table 41. Summary of CV data for microgeographic variation. CV based on averages for each site from averages for each male (as opposed to calls) within a site.

As seen in Figures 37 - 40, variation among males within sites is always greater than variation among sites. In addition, courtship calls exhibit greater among site variation than pursuit calls, and frequency parameters (Figures 37 - 38) exhibit greater variation overall than temporal parameters (Figures 39 - 40). Within individual variation is much lower for courtship calls for spectral parameters, while among individual and among site variation is much larger for courtship calls for both temporal and spectral parameters.

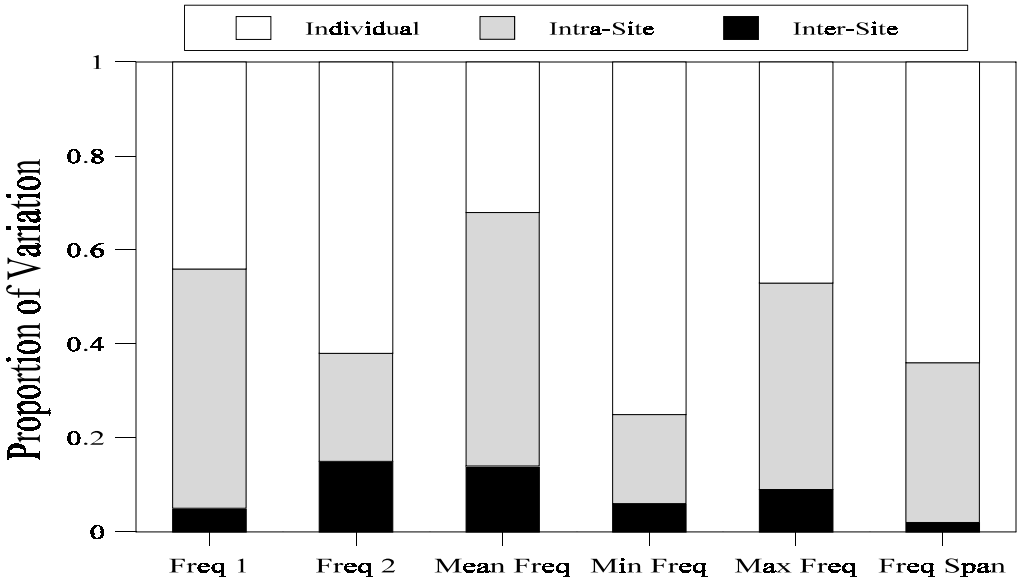

Figure 37. Proportion of variation in courtship calls in each frequency parameter based on the sum-of-squares from the nested MANOVA. White bars indicate variation explained by within male variation, grey bars indicate variation among males and black bars indicate variation among sites.

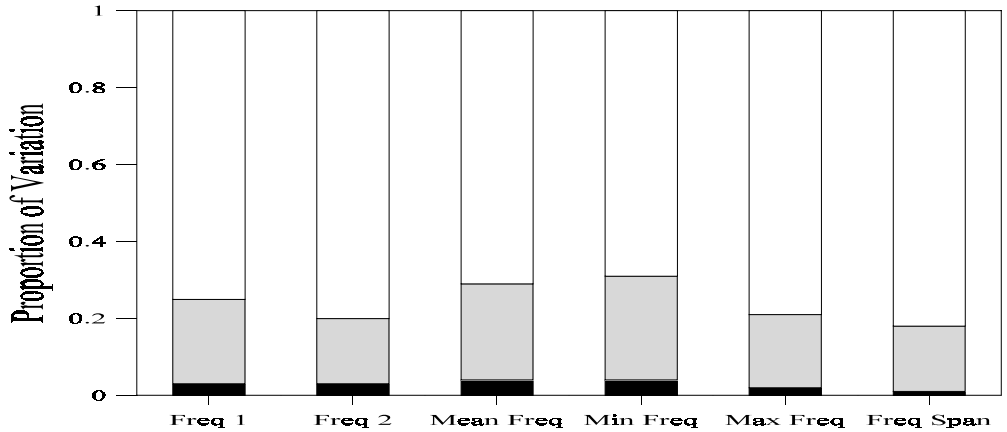

Figure 38. Proportion of variation in pursuit calls in each frequency parameter based on the sum-of-squares from the nested MANOVA comparing sites.

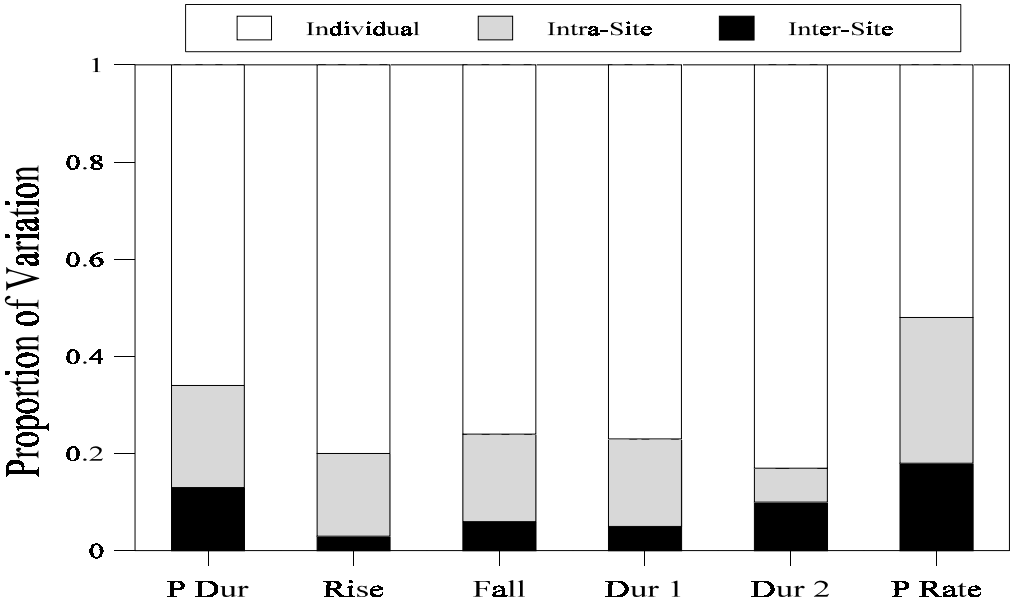

Figure 39. Proportion of variation in courtship calls in each temporal parameter based on sum-of-squares of the nested MANOVA.

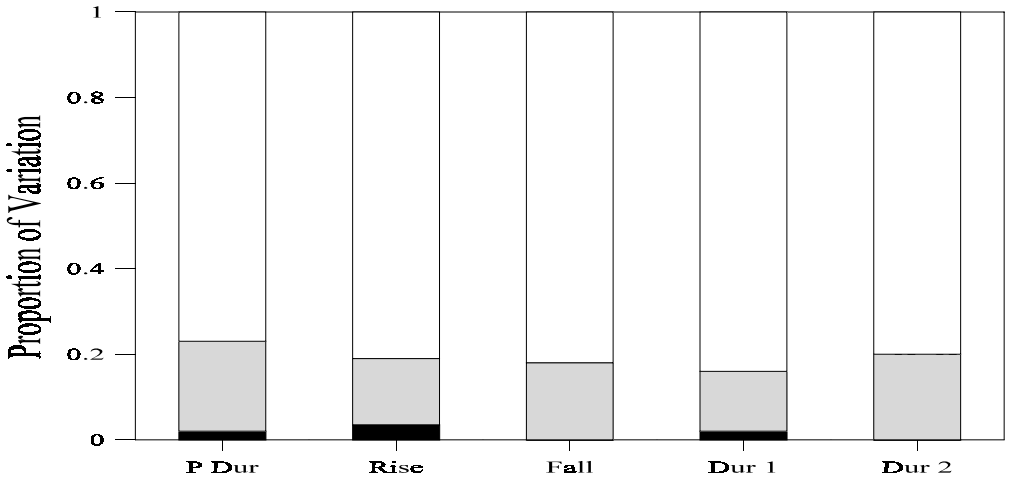

Figure 40. Proportion of variation in pursuit calls in each temporal parameter based on sum-of-squares of the nested MANOVA.

Macrogeographic

Differences among subspecies were examined using an expanded data set that included males with 5 or more pulses per context. The sample sizes for Mexico and Oklahoma were very small (see Table 31), but nested ANOVAs (fish nested within site nested within subspecies) indicated significant differences among subspecies for all parameters for courtship calls and all but rise time, call duration, and pulse rate for pursuit calls (Table 42). DFA classified pursuit calls correctly in 66% of the cases (random expectation = 33%) and courtship calls correctly in 78% of the cases (random expectation = 50%). Stepwise DFA indicated that pulse duration was the most important parameter for classifying pursuit calls to subspecies while pulse duration, rise time and fall time were most important for classifying courtship calls to subspecies (Table 42).

Call Parameter	Pursuit ANOVA	Courtship ANOVA	Pursuit DFA	Courtship DFA
Pulse Duration (msec)	**0.000**	**0.000**	1.10	1.85
Rise Time (msec)	0.009	**0.000**		-1.04
Fall Time (msec)	**0.000**	**0.000**	-0.46	-1.84
Mean Frequency (Hz)	**0.000**	**0.000**	0.64	
Maximum Frequency (Hz)	**0.000**	**0.000**	-0.65	0.71
Call Duration (msec)	0.36	**0.000**	-0.14	0.45
Minimum Frequency (Hz)	**0.000**	**0.000**	-0.61	
Dominant Frequency (Hz)	**0.000**	**0.000**		
Pulse Rate (pulses/sec)	0.20	**0.000**		
Nested MANOVA	**0.001**	**0.001**	n/a	n/a

Table 42. Probabilities from macrogeographic differences from nested ANOVAs based on call averages. Significant p-values ($\alpha = 0.006$ Dunn-Šidák correction) in **bold**. MANOVA results based on pulses with $\alpha = 0.05$. Factor loadings for the first factor from DFA based on call averages for classifying to subspecies. Empty cells indicate parameters removed during stepwise DFA.

Overall Trends

Duration 1 and duration 2 are least variable across all levels of analysis, while pulse duration has low levels of variation only within individuals (Table 43). Rise time is least variable within individuals and sites, while fall time is least variable among sites and among subspecies. Minimum frequency is most variable across all levels and pulse rate is most variable across most levels for pursuit calls.

Parameter	Within Individual	Intra-Site	Inter-Site
Duration 1	/ =	/ =	/ =
Duration 2	/ =	/ =	/ =
Pulse Duration	/ =		=
Rise Time	/	/ =	
Fall Time			/
Mean Frequency			+
Maximum Frequency			
Call Duration	+		+
Minimum Frequency	^ +	^ +	^ +
Dominant Frequency		^ +	^ +
Second Frequency			
Frequency Span	^	+	
Pulse Rate	^ +	^	^

Table 43. Summary of most and least variable parameters at each level of variation based on CVs. ^ indicates most variable parameters for pursuit calls. / indicates least variable parameters for pursuit calls. + indicates most variable parameters for courtship calls. = indicates least variable parameters for courtship calls.

Post-hoc univariate tests from the MANOVA tests and the individual ANOVA tests yield similar differences among call parameters at each level (Table 44). Due to similarity across data sets and statistical tests, only the individual ANOVA results for call averages are summarized. Pulse duration, mean frequency, maximum frequency and dominant frequency were significantly different for both pursuit and courtship calls for every level of analysis. Fall time and minimum

frequency were different for the majority of comparisons. Pulse rate, call duration and rise time were occasionally different.

Parameter	Intra-Site		Within Watershed		Inter-Site		Among Subspecies	
Pulse Duration	^	+	^	+	^	+	^	+
Rise Time					^	+		+
Fall Time		+	^	+	^	+	^	+
Mean Frequency	^	+	^	+	^	+	^	+
Maximum Frequency	^	+	^	+	^	+	^	+
Call Duration				+	^	+		+
Minimum Frequency	^		^		^	+	^	+
Dominant Frequency	^	+	^	+	^	+	^	+
Pulse Rate						+		+

Table 44. Summary of parameters with significant differences in univariate tests in MANOVAs. ^ indicates parameters important for pursuit calls. + indicates parameters important for courtship calls.

DFA results were largely similar for all data sets. Only data from call averages is summarized in Table 45. Pulse duration and minimum frequency were important for all comparisons, while dominant frequency and pulse rate were only important for courtship calls. Mean frequency, maximum frequency, rise time, fall time and call duration were important for some comparisons. There are differences between the contexts at every level of analysis.

Parameter	Intra-Site		Within Watershed		Inter-Site		Among Subspecies	
Pulse Duration	^	+	^	+	^	+	^	+
Rise Time		+	^			+		+
Fall Time		+	^		^	+	^	+
Mean Frequency	^	+	^	+	^	+	^	
Maximum Frequency	^	+		+	^	+	^	+
Call Duration		+		+	^		^	+
Minimum Frequency	^	+	^	+	^	+	^	+
Dominant Frequency		+		+		+		
Pulse Rate		+		+		+		

Table 45. Summary of parameters used to classify calls correctly in DFA for call averages. ^ indicates parameters important for pursuit calls. + indicates parameters important for courtship calls.

Community Composition

In addition to variation in calls among sites, there were also differences in community composition and body size among sites. The Oklahoma and Mexico populations had substantially different populations (Matthews et al. 1994 and Minckley 1969, respectively. See Table 46 for species lists for each Texas site). The Oklahoma and Texas communities contained the same sunfish species. The largest differences among communities were in minnows (Cyprinidae) and turtles. The Mexico community had only one species in common with Texas populations (largemouth bass, *Micropterus salmoides*) and lacked other sunfish species.

The most notable difference among Texas populations is that Barton Creek had substantially more *L. auritus* (non-native, red-breasted sunfish) than any other site. *L. auritus* was very rare or non-existent at the other 5 sites, but was often the most common sunfish at Barton creek. This is particularly relevant because of all the *Lepomis* present in central Texas, *L. auritus* overlaps most with *L. megalotis* for nesting habitat preferences (pers. obs.). In other words, *L. megalotis* males likely compete with much larger *L. auritus* males for nest sites. Interestingly, parental male *L. megalotis* at Barton Creek averaged 20 g and 100 mm fork length (FL), while parental males from any other site, including Mexico and Oklahoma, ranged from 44 - 63 g and 123 - 137 mm FL. This allowed Barton males to nest in shallower water and probably reduced competition with *L. auritus* males. This difference in body size likely affected call parameters as body weight was correlated with some call parameters for courtship calls (see Results: Correlations above). ANCOVA statistics testing the effect of weight on differences among sites reveal that weight is not a covariate for pursuit calls ($p = 0.42$) but it is with courtship calls ($p < 0.001$). The body size differences may also have led to unmeasured differences in habitat acoustics as the nests in Barton Creek were often in very shallow (4 cm) water.

Species	BA	BU	ON	WR	WT	WTM
Noturus gyrinus					X	
*Ictalurus punctatus**	X	X	X	X	X	X
Campostoma anomalum	X	X	X	X	X	X
Moxostoma congestum					X	
Cyprinella venusta	X	X	X	X	X	X
Cyprinella lutrensis				X		
Notropis amabilis	X		X			
Gambusia affinis	X	X	X	X	X	X
Etheostoma spectabile		X			X	X
Percina carbonara		X			X	
Micropterus salmoides	X	X	X	X	X	X
Micropterus treculi	X		X		X	
Lepomis cyanellus	X	X	X	X	X	X
Lepomis macrochirus	X	X	X	X	X	X
*Lepomis auritus**	X				X	
Lepomis megalotis	X	X	X	X	X	X
Lepomis miniatus			X			
*Cichlasoma cyanoguttatum**	X				X	

Table 46. Summary of fish communities at each site. In some cases, relative frequency varied even though species present did not. X indicates species present at site. * indicates non-native species.

DISCUSSION

At every level of analysis (individual, intra-site, inter-site, and subspecies), there were significant differences in call parameters. This was true whether call averages, every pulse or only selected pulses were used for any given male included in the analysis. Temporal parameters consistently had lower variation than spectral parameters across all levels of analysis, with the exception of pulse rate and call duration. Mean frequency often had low variation and frequency span often had high variation but these differences were inconsistent across levels of analysis. Pulse duration had low variation within males but was often the most variable of the temporal parameters at all other levels. Pulse duration was also the single most important parameter for distinguishing courtship calls among males and for distinguishing among sites. These results are highly suggestive that pulse duration is used in individual recognition, both in female mate choice and among neighboring males. Although pulse rate is an important call parameter in many other taxa, pulse rate was not significantly different at any level nor was it useful for classifying class correctly at any level. Similarly, although call duration is significantly different among pursuit and courtship calls, it is not important for distinguishing calls among males or among sites. In striking contrast to longear sunfish, spectral parameters are typically least variable in frogs and toads and often useful for discriminating among individual frog (e.g. Bee et al. 2001).

Data from frogs suggests that lower variation is related to parameters that are constrained by morphology (Castellano & Giacoma 1998; Cocroft & Ryan 1995; Ryan 1988). In frogs, frequency and, occasionally, amplitude are directly linked to specific morphological features, while temporal parameters, such as pulse duration and rise time, are controlled more by behavior (Ryan & Wilczynski 1991). Results of my study imply that temporal characters in longear sunfish are more highly constrained (morphologically or physiologically) than are spectral characters - exactly opposite of the pattern found in frogs. Though the sound production mechanism in longear sunfish is unknown, this provides valuable insights as to the type of mechanism. Sound production in fishes typically involves either a strumming or stridulation mechanism which could be constrained in pulse duration or pulse rate by the ability to activate the musculature, but would produce a broad band spectral structure. The results of my study are consistent with a stridulatory mechanism.

Interestingly, there is a similar inverse relationship in which acoustic components transmit best in different media. In air, the temporal components degrade more than the spectral components. In water, the spectral components degrade more than the temporal components. In other words no matter the taxa, the most reliable part of the signal is also the most constrained.

Distress and release calls show similar patterns of contrast relative to

advertisement calls in frogs, as well as birds and mammals. Distress and release calls, both of which are used with heterospecifics, are similar across taxa while advertisement calls are species-specific (Hödl & Gollman 1986; Klump & Shalter 1984; Littlejohn 1999; Maynard-Smith 1965). Pursuit calls in longear sunfish, therefore, are expected to be more general as they are used with heterospecifics as well as conspecifics. In fact, pursuit calls are relatively similar across all the sunfish species (pers. obs.), while courtship calls vary significantly (Gerald 1971). In addition, courtship calls may be subject to female choice while pursuit calls are not. The results of my study are in accord with these patterns. DFA and PCA results suggest that pursuit calls are less different both among males and among sites than courtship calls. This is expected theoretically for several reasons. First, pursuit calls are used with both heterospecifics and conspecifics and need only to convey the presence and annoyance of a parental male. Second, courtship calls are presumably under sexual selection by females during mate choice and are likely to convey more complex information. Third, individual male recognition is likely to be more important to a prospective mate than to a wandering raider.

In general, geographic variation in communication systems can be shaped by several types of forces – gene flow, habitat variation, community composition, population structure or sexual selection. Gene flow and habitat variation can result in clinal variation, while sexual selection can result in seemingly random patterns.

Since many stream populations are isolated, genetic drift among populations may also contribute to geographic differentiation. Geographic distance, or gene flow, does not explain the variation among sites, so other forces must be examined to explain the geographic variation. My study explored habitat variation and differences in community composition.

Studies of the habitat acoustics of each site indicate that there are no substantial differences among sites in sound transmission (see Chapter 4). There are differences in the level of background noise, however, especially at Waller Creek which has 10 - 30 dB more noise at 50 - 100 Hz than any other site (see Figure 26 in Chapter 4). Waller Creek courtship calls did have longer pulse duration and lower frequencies than calls from other sites. Habitat differences do not appear to drive geographic variation in calls, other than a possible effect of excessive background noise in Waller Creek. Calls from Waller Creek had longer pulse duration and lower frequencies on average than did calls from other sites. Community composition differences may also contribute to geographic variation as seen by the abundance of redbreast sunfish and the small body size of parental males in Barton Creek. Calls from Barton Creek had more high frequency components than calls from other sites.

There is microgeographic variation in acoustic signals of *Lepomis megalotis*, with courtship calls showing more geographic and inter-individual

variation but less within-individual variation than pursuit calls. Pursuit calls are used with many species and are likely under selection for a generalized signal understood across taxa. Habitat differences, except possibly noise pollution, do not explain the geographic variation. Differences in community composition might explain the differences seen at one site but not at all sites.

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